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MOISTURE RETENTION BY SOME IRRIGATED SOILS AS RELATED TO SOIL-MOISTURE TENSION[1]

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INTRODUCTION

The processes of depletion and replenishment of soil moisture have received considerable attention from agricultural scientists because of the dependence of plant growth on the soil-moisture supply. The maximum amount of moisture that can be stored in soil in the field and the degree of dryness to which plants can reduce the moisture content of soil are the limits that determine the range of moisture available to plants. Numerous single-valued soil-moisture constants, such as moisture-holding capacity, moisture equivalent, field capacity, and the various wilting percentages, have been used for indicating the capacity of soils to retain water. The possible advantages of expressing moisture retention in terms of the physical condition of the moisture in soil or in terms of the security with which the water is retained as expressed by some energy or thermodynamic scale have long been considered (*4*).[2]

Some of the scales that have been proposed for this purpose will be discussed, but it is the main object of this paper to present data on the relation between the equivalent negative pressure or tension in the soil water and the moisture content for 71 soil samples collected by Furr and Reeves. On these samples the collectors[3] made careful determinations of the moisture equivalent, the first permanent wilting percentage, and the ultimate wilting percentage, and stated:

> With few exceptions the soil samples were taken from the top foot of soil, and most of them were from cultivated, irrigated orchards or fields. A few samples were from uncultivated desert or brushlands. The samples were air-dried and screened through a round-hole 2-mm. screen.

APPARATUS AND PROCEDURE

The pressure-membrane apparatus (*12*) was used to obtain moisture data at tensions above 1 atmosphere. This is a modification of ultrafiltration apparatus which has been used by Woodruff (*21*) for the same purpose. The extraction cells were the same as those already described (*12*), consisting of a Visking[4] membrane supported on a brass screen and plate with a cylindrical soil chamber 29 cm. in diameter and 1.3 cm. high. Moisture was extracted by water pumped nitrogen supplied from a storage cylinder.[5]

[1] Received for publication March 3, 1943. Cooperative investigation of the U. S. Regional Salinity Laboratory, Bureau of Plant Industry, Soils, and Agricultural Engineering, Riverside, Calif.; 11 Western States; and the Territory of Hawaii.

[2] Italic numbers in parentheses refer to Literature Cited, p. 234.

[3] FURR, J. R., and REEVES, J. O. THE RANGE OF SOIL MOISTURE PERCENTAGES THROUGH WHICH PLANTS UNDERGO PERMANENT WILTING IN SOME SOILS FROM SEMIARID IRRIGATED AREAS. 1942. [Unpublished manuscript.]

[4] The Visking Corporation, Chicago, Ill.

[5] A small refrigeration compressor, on which tests have just been completed, has been found to supply ample quantities of compressed air for pressure-membrane work and has been operated at pressures up to 420 pounds in.$^{-2}$.

During moisture extraction most soils undergo a certain amount of shrinkage that tends to pull the soil out of contact with the membrane. To prevent this, a soft-rubber diaphragm actuated by a 5 pound per square inch pressure differential was used to hold the soil against the membrane. This pressure differential was obtained by inserting in the line between the pressure source and the soil chamber a mercury

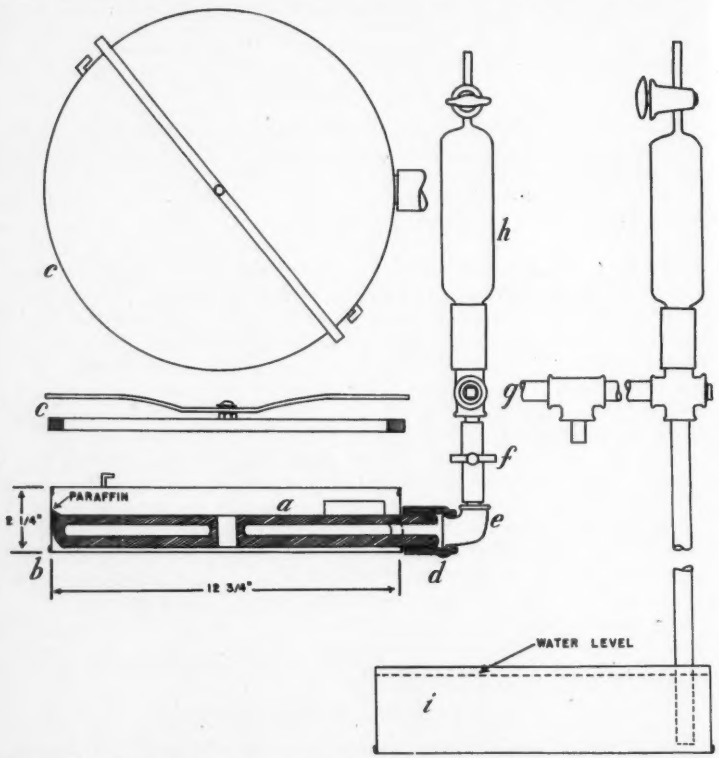

FIGURE 1.—Suction-plate apparatus for determining single moisture-retention values for soils in the 1-atmosphere tension range: *a*, Ceramic cell with porous upper surface; *b*, galvanized-iron box; *c*, box lid with spring clamp and sponge-rubber gasket; *d*, ⅞-inch automobile radiator hose; *e*, ⅜-inch galvanized pipe L with ⅜- to ¼-inch pipe bushing, which has a section of 7/16-inch copper tubing soldered in place; *f*, ⅜-inch (inside diameter) vacuum rubber tubing with pinch clamp; *g*, manifold for making connection to a number of cells; *h*, glass air trap; *i*, water reservoir.

U-tube fitted with a bypass valve. The diaphragm pressure was obtained from the pressure-inlet side of the U-tube and was applied by closing the bypass valve and venting the soil chamber. To prevent undesired compacting and puddling effects on wet soils, the diaphragm pressure was not applied until the moisture content of the sample was reduced to somewhere near the 1-atmosphere percentage. In future work it is contemplated that the mercury U-tube will be replaced by a water U-tube.

Moisture-retention data at tensions between zero and 1 atmosphere were obtained either with pressure-plate or suction-plate apparatus. The pressure-plate apparatus is identical in principle with the pressure-membrane apparatus but makes use of a porous ceramic plate instead of the cellulose membrane. The suction-plate apparatus used is shown in figure 1. The porous ceramic cell [6] is of single-piece construction and is mounted in a galvanized-iron box. The lid is fitted with a sponge-rubber gasket and a spring clamping bar. The cell spout extends from a hole in the box and connects through various fittings to the manifold. This manifold has connections for as many of the suction-plate units as are needed and slopes upward toward the pipe cross and the separatory funnel that is used as an air trap. A pipe extends downward from the air trap to a free water surface, the elevation of which determines the negative pressure at the porous surface. The suction, of course, can be produced when desired by a controlled vacuum system.

The procedure for obtaining all of the moisture-retention data presented in this paper was as follows: A layer of screened, air-dried soil was placed on the porous moisture-extracting surface; the soil was wet thoroughly with an excess of distilled water, and then the moisture was extracted until the moisture tension in the soil increased to a constant predetermined equilibrium value and moisture outflow from the sample ceased. For the determination of single moisture-retention values, a number of soil samples were brought to equilibrium in the same extraction cell, the moisture-content determinations being made by drying to constant weight at 105° C. Moisture retention was expressed as percentage of dry weight so as to be comparable with moisture-equivalent and wilting data.

The soil samples were kept separate on the porous plate by placing them in thin-walled brass rings 5.4 cm. in diameter and 1 cm. high. This permitted 12 to 14 determinations per ground cell. Rings 2 cm. high can be used when larger soil samples are desired.

When moisture-retention curves were desired, the entire pressure-membrane or pressure-plate cell was loaded with one soil sample. The moisture percentage at any desired number of equilibrium-tension values can be calculated from the combined record of the moisture extracted at each succeeding tension increment, the final moisture content, and the total dry weight of the sample.

The amount of moisture a soil will retain at a given tension depends somewhat on the time allowed for wetting the air-dried sample. Some sandy soils show no increase in moisture retention for wetting time beyond 15 minutes, but some fine-textured soils require as much as 18 to 24 hours before the moisture retained is independent of the wetting time. An overnight wetting time of 16 to 18 hours was used for the determinations reported in this paper.

For all except very impermeable soils, 4 to 6 hours is ample time for a 1- to 2-cm. layer of saturated soil to come to equilibrium after the pressure differential is applied to the porous ceramic plates used. The time required for outflow equilibrium in the pressure-membrane apparatus is indicated by the curves in figure 8, which will be discussed later.

[6] Ground cell K 939-B, General Ceramics and Steatite Company, Keasbey, N. J.

Unless otherwise indicated, all the soil-moisture tension data presented in this paper were obtained at a temperature of 21° C., and the following pressure equivalents were used: 1 atmosphere=1.013×10^6 dyne cm.$^{-2}$=14.71 pounds in.$^{-2}$=76.39 cm. of mercury=1,036 cm. of water=34.01 feet of water.

FIFTEEN-ATMOSPHERE PERCENTAGE AND THE WILTING RANGE

For the soils used in the first tests of the pressure-membrane apparatus it was found that an extraction pressure of 16 atmospheres reduced the moisture content slightly below the wilting percentage, as determined with sunflowers by Eaton and Horton (*6*). In view of this preliminary experience it was decided to determine the 15-atmosphere percentage for the soil samples collected by Furr and Reeves. Table 1 gives the moisture equivalent, the first permanent wilting percentage, and the ultimate wilting percentage as determined by Furr and Reeves, and in addition gives the moisture retained by these soils at five soil-moisture tension values.

TABLE 1.—*Moisture*[1] *retained by soils after moisture-extracting treatments*

Soil type	Soil accession No.	Moisture equivalent	First permanent wilting	Ultimate wilting	Moisture retained at indicated soil-moisture tension				
					Centimeters of water				Atmospheres
					250	345	440	518	15
Coarse soils:		*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Washed and screened sand, 10-20 mesh	57	1.3	1.2	0.7	1.2	1.2	1.2	1.1	0.8
Washed and screened sand, 20-30 mesh	56	1.4	1.3	.7	1.3	1.2	1.3	1.2	.9
Washed and screened sand, below 30 mesh	55	1.9	1.4	.9	1.9	1.5	1.7	1.6	1.0
Tujunga sand	52	2.6	1.8	1.2	2.3	2.1	2.2	2.1	1.4
Hanford sand	51	4.8	2.9	1.9	5.0	4.5	4.3	4.1	2.2
Ramona sand	54	5.0	2.9	2.2	5.2	4.4	4.5	4.2	2.0
Indio loam	76	5.2	2.6	1.6	5.3	4.6	4.3	3.8	1.6
Indio very fine sand	48	5.8	3.2	2.0	5.9	5.0	4.7	4.1	1.9
Dune sand	53	6.0	2.6	1.9	6.6	5.6	5.4	5.2	2.9
Superstition (leached) sand	50	6.6	2.4	1.5	6.5	------	4.8	4.4	1.9
Holland sandy loam	41	6.9	4.2	3.2	7.6	6.4	6.2	5.5	2.7
Indio very fine sandy loam	70	7.3	3.2	1.9	8.2	6.9	6.4	5.7	2.2
Indio loam	75	7.4	2.8	1.9	7.5	6.2	6.2	5.1	1.9
Placentia sandy loam	43	7.4	3.9	3.2	8.1	6.7	6.4	6.0	2.5
Indio fine sandy loam (6 feet)	82	7.7	3.9	2.5	9.2	8.0	7.5	6.6	2.7
Hanford fine sand	47	8.0	3.8	2.5	8.8	7.6	7.3	6.8	2.3
Fresno fine sandy loam	40	8.9	3.7	2.5	10.2	8.5	8.1	7.5	2.3
Ramona fine sandy loam	37	9.2	5.2	3.7	10.1	8.3	8.3	7.8	3.5
Tujunga Stony sand	58	9.8	5.2	3.8	10.2	9.1	8.8	8.1	4.3
Indio fine sandy loam (5 feet)	81	9.9	5.2	3.2	12.3	10.7	10.0	8.8	3.1
Placentia clay loam	17	10.9	6.0	4.7	11.8	10.0	9.8	8.7	5.6
Hanford gravelly sandy loam	26	11.3	5.4	3.5	12.6	9.8	9.5	9.0	3.5
Hanford sandy loam	42	12.4	4.8	3.6	14.2	11.7	10.6	9.7	2.9
San Joaquin sandy loam	46	12.5	5.9	4.1	14.1	12.1	12.2	11.6	4.3
Greenfield loam	N4	12.7	6.3	5.1	17.3	14.5	14.2	13.1	5.4
Tujunga fine sandy loam	39	13.2	5.5	4.1	20.3	15.6	13.8	12.2	3.5
Yolo loam	31	14.3	8.4	6.7	16.1	12.6	12.7	11.6	7.1
Hanford loam	29	14.5	6.0	4.0	16.9	14.0	13.2	11.8	4.4
Placentia loam	28	14.8	7.7	5.3	16.9	14.0	13.4	12.6	5.7
Coachella very fine sand	49	15.2	5.7	4.0	18.1	14.5	13.2	12.1	3.8
Indio loam (4 feet)	74	15.4	6.1	3.3	18.0	------	14.5	13.2	3.8
Altamont clay	2	15.6	6.8	5.2	19.4	15.4	14.7	13.4	5.7
Yolo fine sandy loam	38	15.4	8.4	6.2	14.7	12.6	12.1	12.0	5.5
Total[2]	------	279.6	137.8	98.0	318.3	265.3	254.2	233.1	99.6

[1] Expressed on a dry-weight basis.
[2] Omitting soils 50 and 74.

TABLE 1.—*Moisture retained by soils after moisture-extracting treatments*—Con.

Soil type	Soil accession No.	Moisture equivalent	First permanent wilting	Ultimate wilting	Moisture retained at indicated soil-moisture tension				
					Centimeters of water				Atmospheres
					250	345	440	518	15
Fine soils:		*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Madera sandy loam	45	16.0	6.6	4.8	16.0	13.2	12.9	11.8	4.5
San Joaquin loam	33	16.2	8.1	6.3	18.0	15.1	15.4	14.4	6.5
Ramona loam	27	16.6	8.3	5.6	18.7	15.4	15.1	14.3	6.0
Indio fine sandy loam (5 feet)	79	16.9	6.8	3.8	19.9	17.0	16.0	14.9	4.6
Indio fine sandy loam (1 foot)	77	17.5	5.9	3.5	21.9	17.7	16.3	14.7	4.2
Madera loam	32	17.6	9.9	7.7	22.1	18.0	18.5	16.6	8.4
Hanford fine sandy loam	36	17.8	6.7	4.7	22.5	18.0	16.9	15.2	4.3
Altamont clay loam	14	18.4	10.0	8.8	19.0	16.1	16.4	15.3	9.1
Indio very fine sandy loam (5 feet)	69	19.0	5.6	4.0	21.2	18.3	17.7	15.9	4.8
Ramona clay loam	15	19.0	9.3	6.3	23.1	19.4	18.9	17.5	6.7
Indio loam (3 feet)	73	20.2	7.0	4.2	24.2	------	19.8	17.9	5.0
Antioch silty clay loam	22	20.9	10.7	9.0	25.2	20.8	20.0	17.9	9.5
Chino loam	30	21.0	10.2	7.5	23.6	19.7	19.8	18.4	8.0
Indio very fine sandy loam (4 feet)	68	21.2	6.9	4.3	23.9	------	20.1	18.3	5.2
Yolo clay loam	16	21.3	12.3	10.4	23.7	20.4	19.8	18.1	10.2
Madera clay loam	18	21.7	11.7	8.2	24.0	21.3	21.4	20.2	8.8
Indio fine sandy loam (4 feet)	80	22.8	8.8	5.3	27.0	23.7	22.5	20.9	6.4
Indio clay loam	85	22.9	8.9	5.9	29.2	24.6	23.0	20.6	6.5
Indio loam (1 foot)	71	23.2	8.0	5.1	27.1	22.8	21.9	20.0	6.1
Montezuma clay	4	24.4	13.2	10.5	22.8	20.2	19.8	17.6	11.3
Hanford silty clay loam	25	24.4	14.3	12.1	29.5	24.3	25.4	22.8	13.2
Montezuma clay	8	25.9	13.3	10.1	30.0	25.9	27.2	24.9	12.7
Indio fine sandy loam (2 feet)	78	26.1	11.5	5.8	31.2	------	26.1	24.1	7.0
Fresno loam	34	26.8	14.2	9.6	34.4	30.5	29.3	27.2	10.7
Dublin clay	1	27.4	16.4	13.2	30.7	27.6	27.3	24.0	14.2
Chino silty clay loam	23	27.6	14.4	10.4	30.5	26.8	25.9	24.3	11.0
Antioch clay	5	29.5	17.8	15.5	38.6	28.5	29.0	26.9	16.5
Indio loam (2 feet)	72	30.3	8.8	5.7	37.5	32.5	31.4	27.9	6.7
Yellow clay loam (Stevens No. 2)	20	31.0	20.2	16.9	34.5	31.2	31.1	29.7	18.4
Ducor clay	10	31.2	17.1	14.4	35.3	32.0	32.0	28.7	16.5
Merced loam	35	32.0	16.4	11.7	39.5	36.4	34.9	32.5	13.4
Diablo clay	3	34.1	18.2	15.0	33.1	34.0	33.9	31.0	17.7
Chino silty clay loam (heavy phase)	24	37.1	22.4	19.2	40.5	35.6	36.5	33.9	21.1
Chino silty clay	12	37.6	23.2	20.1	42.8	40.8	39.5	36.1	21.9
Portersville clay	7	40.2	21.2	17.1	46.4	41.5	43.5	41.2	23.2
Olympic clay	9	41.8	24.4	19.9	48.0	42.6	43.1	40.2	23.6
Chino silty clay loam	13	43.2	23.3	14.4	53.1	48.9	47.0	44.0	15.0
Yolo clay	6	45.9	29.6	23.6	52.3	45.1	48.1	43.5	26.2
Total [1]		918.2	476.2	366.3	1,061.7	926.4	917.4	843.1	467.9

[1] Omitting soils 68, 73, and 78.

Figure 2 is a scatter diagram showing the relation of the 15-atmosphere percentage to the wilting range. Vertically placed pairs of points give the position of the ultimate and the first permanent wilting percentage of each soil on the moisture scale. The intersection of a vertical line connecting a pair of points with the diagonal locates the 15-atmosphere percentage with respect to the wilting range. It is seen that with but comparatively few exceptions for the soils tested the 15-atmosphere percentage lies in the wilting range. It is estimated that if the complete root system of the wilted plant had been removed from the soil the wilting percentages would have been reduced by 0.2 to 0.3 percent. This reduction would bring the 15-atmosphere percentage of all but 7 of the 71 soils within the wilting range.

The location of the 15-atmosphere percentage in the wilting range may be indicated by another method. The soils in table 1 have been divided into a coarse group (moisture equivalent less than 16 percent) and a fine group (moisture equivalent 16 percent or higher). Totals of the data are given for all of the soils in the two groups except the five for which the data are incomplete. From these totals it is seen that for the coarse group the 15-atmosphere percentage lies in the wilting range and only 0.04 of the wilting range from the ultimate

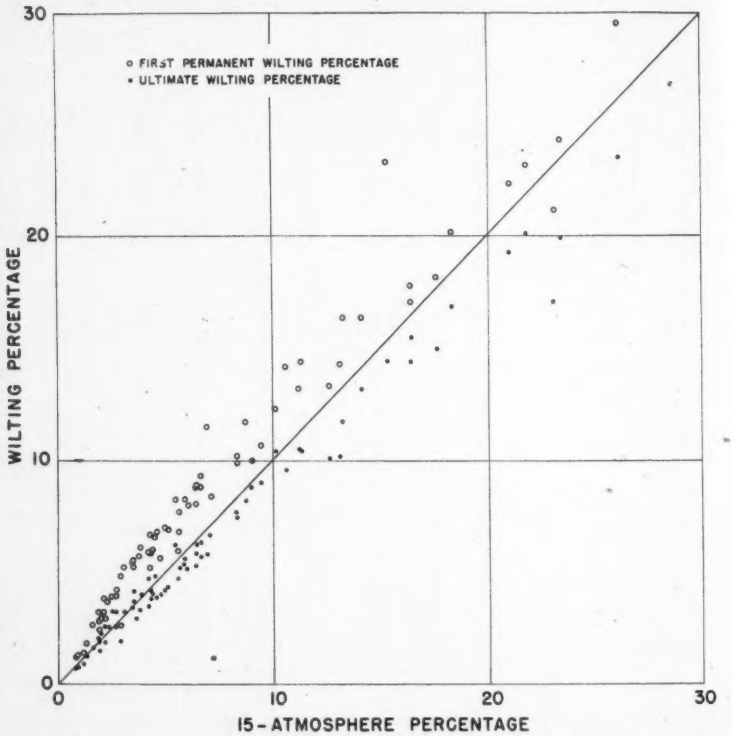

FIGURE 2.—A scatter diagram showing the relation of the 15-atmosphere percentage to the wilting range.

wilting percentage, and for the fine group the 15-atmosphere percentage is 0.38 of the wilting range from the ultimate wilting percentage.

The problem of getting representative samples was given particular attention. Subsamples were taken in such a way as to cause a minimum of particle-size segregation after "pulling" all of the original sample on a Koroseal-coated cloth. The 15-atmosphere percentages shown in figure 2 and table 1 are the average of triplicate determinations. The coefficient of variation [7] for the determinations was larger for the coarse soils, running as high as 5.0 in some cases, but the average coefficient of variation for the whole group of soils was 1.46.

[7] Standard deviation expressed as percentage of mean.

Determination of the 15-atmosphere percentages was made on 21 individual soil samples in one extraction unit at one time by placing the samples in rubber rings 4.1 cm. in diameter and 1 cm. high. The rings were cut from the inner tube of a bicycle tire. The samples were covered with individual squares of waxed paper when placed in the cell so as to minimize vapor losses during transfer to moisture boxes at the end of a run.

SOIL-MOISTURE TENSION AND THE MOISTURE EQUIVALENT

The scatter diagrams in figure 3 show the relation between moisture equivalent as determined by Furr and Reeves and the moisture retained when these soils are wetted and then brought to equilibrium on the suction plate at the four tension values 250, 345, 440, and 518 cm. of water. The determinations were made in triplicate. The coefficients of variation calculated for the 518-cm. determinations were not related to texture and had an average value of 1.50. It is evident that on an average there is a fairly close relation between

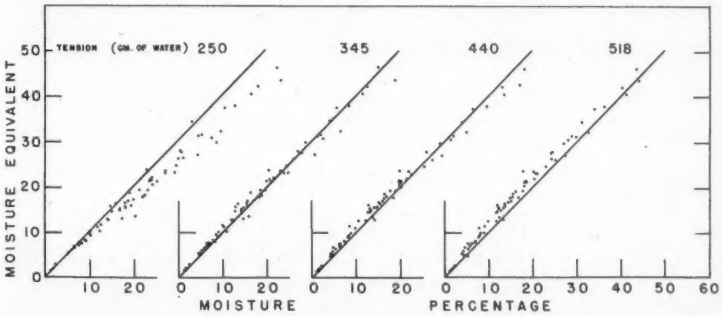

FIGURE 3.—Scatter diagrams showing the relation of the moisture equivalent to the moisture retained by the same group of soils at soil-moisture tensions of 250, 345, 440, and 518 cm. of water. Comparison of the change produced by the various tension increments is aided by the 45° reference lines.

moisture equivalent and the moisture retained at the moisture tension of 345 cm. of water (⅓ atmosphere).

The totals in table 1 indicate that the ⅓-atmosphere percentage is slightly lower than the moisture equivalent for the coarse soils and slightly higher than the moisture equivalent for the fine soils.

It will be noted that there are inconsistencies in table 1. At moisture tensions of 345 and 440 cm. of water, a lower moisture content was found at the lower tension for some of the soils. The authors feel that these inconsistencies were caused by sampling error and do not indicate an inherent lack of precision in the suction-plate procedure, since there was excellent agreement among the triplicate determinations (coefficient of variation, about 1.5). Chronologically the moisture-retention values for the soils at 345 cm. of water tension were the last data determined in the table, and although considerable care was used in subsampling, the inconsistencies in the table seem to indicate that repeated subsampling shifted the texture of some of the stock samples toward lower moisture retention.

TEMPERATURE EFFECT ON MOISTURE RETENTION

Because of the evidence in the literature that temperature has a definite effect on moisture retention, it was felt that part of the scatter in figures 2 and 3 might arise from the fact that the various moisture-equivalent and wilting determinations were made at different temperatures. To get information on this point, 12 soils, covering a wide texture range, were selected from the laboratory-stock samples and the Furr and Reeves collection. Triplicate determinations of the ⅓-atmosphere percentage and the 15-atmosphere percentage were made for each soil at 4 different temperatures. The results of these measurements are given in table 2 and figure 4. Slope and intercept values for least-square straight lines are given in table 2, and these lines are shown in figure 4 along with the experimental points. With but one exception the slopes were negative, as would be expected from the effect of temperature on surface tension. The change in moisture retention per degree of change in temperature increased from coarse to fine texture, but appeared not to be linearly related to the moisture retention of the various soils at any given temperature and tension.

TABLE 2.—*Effect of temperature on moisture retained at ⅓ and 15 atmospheres*

Soil type	Accession No.	Moisture retained at ⅓ atmosphere and indicated temperature (°C.)					$\frac{dPw}{dt}$ [1]	Moisture retained at 15 atmospheres and indicated temperature (°C.)					$\frac{dPw}{dt}$ [1]
		[1] 0	12.2	21.2	29.7	37.2		[1] 0	12.4	21.1	29.5	37.5	
		Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*		*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	
Tujunga sand	52	2.76	2.47	2.42	2.23	1.99	−.0193	1.66	1.46	1.25	1.23	1.00	−.0167
Placentia sandy loam	43	6.10	5.94	5.80	5.63	5.60	−.0144	3.49	3.15	3.03	2.78	2.55	−.0244
Hanford gravelly sandy loam	26	8.45	8.28	8.50	8.30	8.46	.0041	3.88	3.45	3.49	3.31	2.82	−.0245
Placentia loam	28	12.62	12.48	12.41	12.16	12.24	−.0118	6.36	5.79	5.72	5.39	[2] 4.88	−.0363
Sagemoor fine sandy loam	S–40–10	11.90	11.68	11.64	11.28	11.35	−.0163	6.92	6.18	5.80	5.25	4.79	−.0563
Indio very fine sandy loam	S–40–4	18.99	18.31	17.86	17.98	16.87	−.0494	6.80	6.49	6.23	6.00	5.83	−.0264
Chino loam	30	18.78	18.45	18.39	17.78	17.96	−.0252	8.91	8.20	7.94	7.41	6.94	−.0514
Billings clay	S–40–7	22.92	22.15	20.66	20.82	19.81	−.0823	9.41	8.77	8.56	8.13	7.66	−.0448
Altamont clay loam	14	15.36	15.32	15.28	14.86	15.28	−.0070	10.28	9.27	9.46	8.74	[2] 7.90	−.0572
Meloland clay	S–40–2	28.25	28.00	27.60	27.51	27.32	−.0257	17.11	15.63	14.93	14.13	12.87	−.1082
Antioch clay	5	28.29	27.67	26.67	26.31	26.00	−.0649	20.33	18.28	16.79	15.76	14.06	−.1634
Yolo clay	6	44.73	44.37	41.80	42.83	41.81	−.0808	30.75	28.20	26.04	24.96	22.69	−.2102

[1] Values taken from least-square equation having the form $Pw=a+bt$, where Pw represents moisture percentage, t represents temperature, $a=Pw$ for $t=0$ and $b=dPw/dt$.
[2] Values calculated by C. H. Wadleigh, using the missing-plot technique.

SOIL-MOISTURE RETENTION CURVES

Curves showing the relation between the security with which water is held by soil and the amount of water in the soil are being increasingly used in soils work because of their relation to pore-size distribution, structure, and the nature and extent of the soil surface (*5*, *9*).

The curves shown in figure 5 were obtained on air-dried and screened soil samples, this being the normal preparation for moisture-equivalent and wilting-point determinations. The jog in the curves at the 1-atmosphere percentage occurs at the juncture between pressure-plate and pressure-membrane data. With one exception for the curves shown, the discrepancy is less than 0.5 percent and is

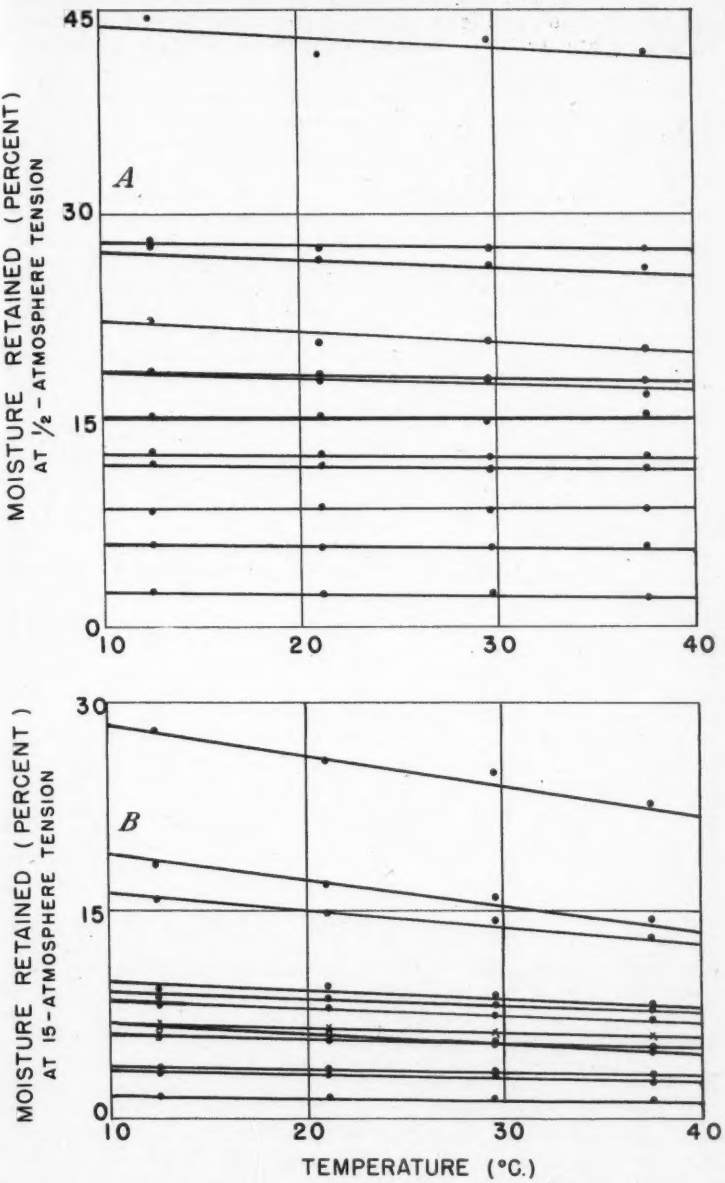

FIGURE 4.—Effect of temperature on the moisture retained by a group of soils at one-half atmosphere (*A*) and 15 atmospheres (*B*) of soil-moisture tension.

believed to be due to soil differences or other imperfection in experimental procedure and is not to be attributed to the change from the ceramic plate to the cellulose membrane. Curves obtained on

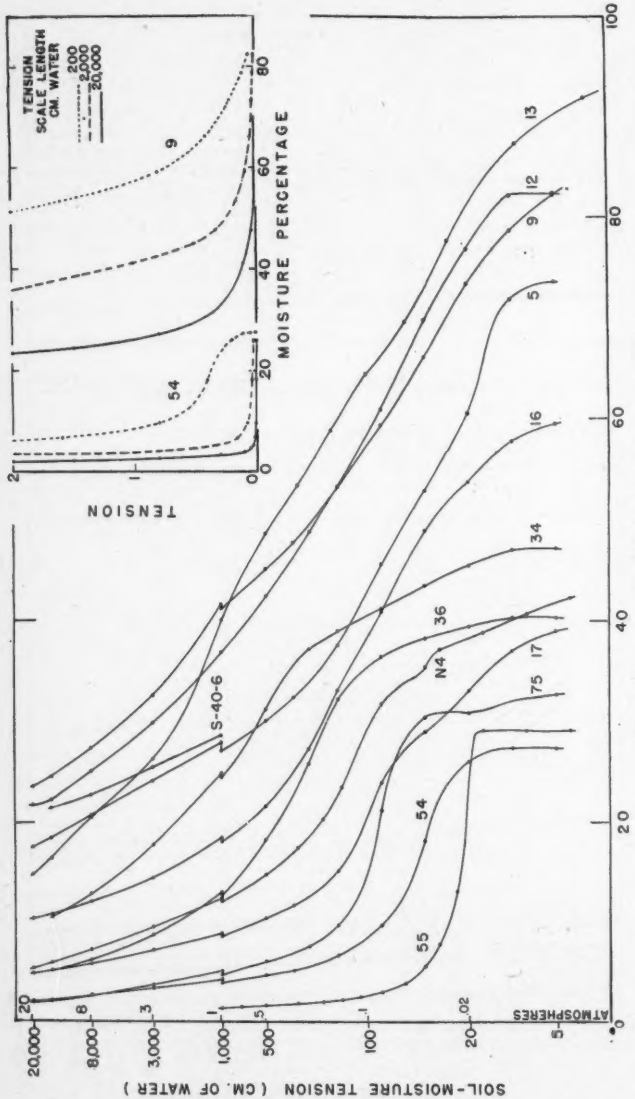

FIGURE 5.—Moisture-retaining properties of soils. The logarithmic scale is helpful for giving a visual comparison over a wide tension range. To show the effect of the kind of scale on the apparent slope of the retention curve, data from the logarithmic curves for soils 54 and 9 are each replotted on three different linear scales in the upper right-hand corner.

duplicate samples agree closely, if care is taken to insure that the samples are as nearly as possible identical. The h gh-tension parts of the curves were obtained by spreading approximately 420 gm. of

dry soil on a circular Visking membrane 29 cm. in diameter, whereas for the low-tension data approximately 55 gm. of soil was spread on a ceramic plate 8.9 cm. in diameter.

A number of interesting facts are brought out by the curves plotted on the logarithmic scale. The marked differences in slope and the crossing of the curves in the high-tension range discourage any attempt to find a general relation between moisture equivalent and the wilting percentage. It is apparent that some of the curves that coincide at the 15-atmosphere tension are widely separated at lower tensions. Since the position and slopes of the curves at the higher tensions are determined largely by the kind and amount of soil colloid, it is likely that moisture-retention data on the extracted colloid will have some use in colloid identification work. The Aiken soil is known to have predominantly kaolinitic colloid and in the field has a very narrow range of moisture available for plants, as indicated by the steepness of the moisture-retention curve for the Aiken soil, which is marked S–40–6 in figure 5.

The smooth curves between the experimental points might be somewhat altered if additional points were determined. In the low-tension range the curves are shifted considerably by small changes in the history or physical condition of the sample, but this sensitivity increases the usefulness of the curves for studying the stability of structure as proposed by Childs (*5*). Since the determinations were made on air-dried and screened samples, the curves differ from those that would have been obtained with field structure.

The moisture-retention data shown by the logarithmic curves for soils 54 and 9 in figure 5 are replotted in the upper right-hand corner of the figure on linear scales. This was done to illustrate the effect of the method of plotting on the apparent shape of the curves. The same moisture scale was used for all of the inset curves, but the dotted curves show the retention data for 0–200 cm. of water; the broken curves, for 0–2,000 cm.; and the solid-line curves, for 0–20,000 cm. It is at once apparent that the position of the "knee" of the curve on the moisture axis depends on the scale and the amount of the retention curve being examined. The appearance of rapid change in the slope of the curve in this region has no special biological or physical significance as far as the moisture-retaining characteristics of the soil are concerned.

SOIL-MOISTURE RELATIONS IN THE 1-ATMOSPHERE RANGE

The moisture equivalent has been widely used as an index of moisture retention by soil, and it is interesting to see how this constant is related to the moisture-retention curve.

The work of Schaffer, Wallace, and Garwood (*16*) indicates that the pressure in the soil moisture is zero at the periphery of the moisture-equivalent centrifuge sample. From this boundary condition, the soil-moisture-tension values at successive 1-mm. distances from the periphery or moisture-outflow surface of the centrifuge sample may be calculated (*15*) from the equation $T=(\omega^2/2g)(r_1^2-r_2^2)$ and are found to be successively 0, 101, 201, 301, 400, 498, 596, 692, 789, 884, and 979 cm. of water. Quantities represented by the symbols in the equation are T, tension; ω, angular velocity of centrifuge; g, acceleration of gravity; r_1 and r_2, distances from center of rotation. The

depths of the soil after centrifugation for a number of 30-gm. moisture-equivalent samples were carefully measured, and the majority were found to range from 9 to 10 mm. deep.

TABLE 3.—*Moisture-retention data as related to moisture equivalent, tensiometer range, and field capacity*

Item	Soil accession No.											
	55	54	75	17	N4	36	16	34	5	12	9	13
(1) Moisture equivalent	1.9	5.0	7.4	10.9	12.7	17.8	21.3	26.8	29.5	37.6	41.8	43.2
(2) Average *Pw*[1] from curves in figure 5 over 0.1- to 1.0- atmosphere tension range	1.6	5.0	6.5	10.9	15.5	19.6	23.0	31.5	30.6	43.3	45.9	48.9
(3) Ratio between numbers in item 2 and item 1	.84	1.00	.88	1.00	1.22	1.10	1.08	1.16	1.04	1.15	1.10	1.13
(4) Tension value on curve at *Pw* in item 2	450	400	420	410	420	442	415	483	450	450	450	475
(5) *Pw* at 40 cm. of water tension	5.5	18.1	30.4	29.0	35.4	38.2	48.9	43.4	52.8	69.8	68.3	72.7
(6) Ratio of *Pw* at 40 cm. of water tension to the moisture equivalent multiplied by 2	1.42	1.81	2.05	1.33	1.39	1.07	1.15	.81	.89	.93	.82	.84
(7) Difference between *Pw* at 0.1- and 0.85-atmosphere tension	1.25	4.5	11.6	12.1	16.3	21.0	19.6	13.8	12.8	19.3	15.3	21.1
(8) Difference between *Pw* at 0.1- and 15-atmosphere tension	1.7	6.7	14.9	15.7	23.4	31.0	28.4	29.8	23.8	36.1	33.7	49.4
(9) Ratio between numbers in item 7 and item 8	.74	.67	.78	.77	.70	.68	.69	.46	.54	.53	.45	.43

[1] The symbol *Pw* represents percentage of water in the soil expressed on a dry-weight basis.

It is difficult to say exactly where in the centrifuge soil-cup system the zero-pressure boundary condition applies. If this is taken to be the surface between the screen and the centrifuge case, then about 1 mm. is taken up by the screen and the filter paper, and on the basis of the above calculations this would give a tension of 100 cm. of water at the outer surface of the soil. The moisture equivalent is the average moisture content for the whole centrifuge sample and, therefore, should be the average of moisture values taken from a retention curve at points corresponding to the tension and packing at successive 1-mm. layers of the sample. Since the departure from linear tension distribution is small, it should be possible to approximate the moisture equivalent by averaging the moisture-content values on the moisture-retention curve for the centrifuged sample between the tension limits determined by the distances of the inner and outer soil boundary from the water-outflow surface. The average moisture percentage for the 100 to 1,000 cm. of water-tension range of each of the curves in figure 5 was determined, and these values are given in item 2 of table 3. The ratios of these average values to the corresponding moisture equivalents are given in item 3. The average value ratio is 1.06. These results are about what might be expected, since for most soils centrifugation produces denser packing

and less pore space than existed in the uncentrifuged pressure-plate samples. The curves in figure 5, particularly at lower tensions, show higher moisture retention than would be found if the samples had been compacted in the centrifuge. The foregoing analysis, therefore, supports the view that the moisture equivalent is the average value over approximately the 0.1- to 1.0-atmosphere tension range for a moisture-retention curve that takes into account centrifuge packing effects.

It is becoming increasingly clear that the moisture equivalent cannot be generally used as an index of either the upper (*3, 11*) or the lower [8] (*20*) limit of moisture usable by plants in the field. Moisture equivalent has the advantage of being a definite reproducible quantity not too difficult to determine, but this is insufficient justification for its continued use provided something more closely related to the available moisture range can be found. It is apparent from figure 3 that moisture-retention values in the ¼- to ½-atmosphere ranges are too closely related to moisture equivalent to be of appreciably greater use or significance, except that (1) they are less expensive to determine and (2) they do represent a more definite physical property of the soil moisture. This latter is some advantage since it makes the determination independent of the kind of apparatus used, provided, of course, that the procedure does not alter the condition of the sample. As a substitute for moisture equivalent the ½-atmosphere percentage appears to merit some consideration, but the authors feel that the expression "moisture equivalent" should be used only in connection with determinations made with the Briggs and McLane equipment.

From tensiometer data now available for several soils it appears that field capacity may correspond to a tensiometer reading somewhere near 0.1 atmosphere, but there seems to be no distinctive feature of the tension-time curve following irrigation that can be associated with the condition of field capacity. If further field measurements should indicate that there is a certain tension range that approximates field capacity, it would be possible, by adjusting the height of the sample, the thickness of a standard porous pad under the sample, and the speed, to set up a centrifuge method that would give the average moisture percentage for any section of a moisture-retention curve. The fact that the field capacity depends on the nature and condition of the whole profile, including the initial moisture distribution, the moisture-transmitting properties of the soil, the moisture-retaining properties of the soil, and the amount of water applied, increases the difficulty of basing a field-capacity estimate on a soil sample isolated from the profile.

It might be expected that an estimate of field capacity could be more readily based on a soil sample having field structure than on one that is dried and screened, but the advantages of the latter for routine work are obvious. Centrifuge packing may partly overcome the structural disruption caused by screening, but the ratio of field capacity to moisture equivalent is considerably higher for coarse than for fine soils (*3, 11*). The possibility that a moisture-retention value at a lower tension than the ½-atmosphere percentage may be a better indication of field capacity is suggested by the fact that this tension empties a relatively larger fraction of the pore space for the

[8] See footnote 3, p. 215.

coarse-textured soils than for the fine-textured soils. The numbers given in item 6 of table 3 were obtained by dividing the moisture retained at 40 cm. of water tension (item 5) by twice the moisture equivalent. These numbers when plotted against moisture equivalent correspond closely to Browning's (*3*) field-capacity moisture-equivalent ratio curve when the latter is corrected for the difference between the Gooch crucible and the standard moisture-equivalent procedure. This correspondence indicates that for these 12 soils half the water retained at 40 cm. of water tension by a sample that has been air-dried and screened closely approximates the field capacity as determined by Browning. This agreement may be only fortuitous, but it is possible that further work along this general line may yield a useful field-capacity index.

The curves in figure 5 give basis for an estimate of the fraction of the available range of moisture over which tensiometers can be used. Item 7 in table 3 gives the difference between the 0.1-atmosphere percentage and 0.85-atmosphere percentage, these being common limits between which field tensiometers (*13*) have been found to operate. The figures in item 8 are the difference between 0.1-atmosphere percentage and 15-atmosphere percentage and are a measure of the available range of moisture for the various soils. Item 9 gives the ratios of the numbers in item 7 to those in item 8 and indicates the fraction of the available range over which tensiometers can be used. This fraction is seen to vary from less than 0.5 in the fine soils to about 0.8 in the coarse soils. Under conditions of restricted drainage, this fraction is appreciably increased. For a soil having a permanent wilting percentage of 3.7, which was used in 20-gallon culture cans provided with free drainage, it has been found that the moisture range over which tensiometers operate comprises 0.9 of the available range.[9]

SOIL-MOISTURE TENSION IN THE WILTING RANGE

Since it is not yet possible to measure directly the soil-moisture tension in a sample of soil in the wilting range, some information on the range in tension that corresponds to the wilting range may be obtained indirectly by placing the wilting percentages on the moisture-retention curves (*14*, *21*).

In figure 6 the first permanent wilting percentage and the ultimate wilting percentage as determined by Furr and Reeves have been located on moisture-retention curves determined with the pressure-membrane apparatus. Broken lines indicate where the curves were extrapolated beyond the experimentally determined points. From these results it would seem that neither the first permanent wilting percentage nor the ultimate wilting percentage is closely related to soil-moisture tension.

To get information on the free energy, or pF, at wilting for the Furr and Reeves samples requires consideration of soluble salt content as well as soil-moisture tension. The osmotic concentration of the soil solutions at the wilting points could have been determined by measuring the freezing points on soil solutions extracted from samples in which the sunflowers were wilted. This was not done,

[9] Correspondence with C. S. Scofield concerning work in progress at the Rubidoux Laboratory, Riverside, Calif.

but an estimate of the osmotic pressures involved can be obtained by another method. Column 2 of table 4 gives the moisture percentage of the soils at the beginning of the extraction process used for the determination of the curves in figure 6. The amounts of dissolved solids in the extracts were determined, and the soluble salt content of the soils, expressed as percentage on a dry basis, is given in column 3. Column 4 gives the osmotic concentration of the extracted solution. This latter was obtained by dividing the electrical conductivity expressed in micromhos (at 25° C.) by 28.5.[10] Multiplying these values by the ratios of the initial extraction percentage to the wilting percentages gives an indication of the osmotic pressures at the wilting points.[11] The remainder of the table gives the soil-moisture tension, the osmotic concentration, and the sum of these two at first permanent wilting and ultimate wilting.

TABLE 4.—*Soil-moisture tension and osmotic concentration of the soil solution at wilting*

Soil accession No.	*Pw* before extraction	Soluble salt in soil	Osmotic concentration of extract	First permanent wilting			Ultimate wilting		
				Soil-moisture tension	Osmotic concentration	Soil-moisture tension + osmotic concentration	Soil-moisture tension	Osmotic concentration	Soil-moisture tension + osmotic concentration
		Percent	*Atmos.*	*Atmos.*	*Atmos.*	*Atmos.*	*Atmos.*	*Atmos.*	*Atmos.*
49	65.3	0.06	0.37	8.8	4.2	13.0	23.7	6.0	29.7
74	61.2	.06	.34	8.0	3.4	11.4	35.5	6.3	41.8
79	58.7	.04	.26	7.0	2.2	9.2	28.9	4.0	32.9
73	74.2	.08	.31	9.2	3.3	12.5	27.0	5.5	32.5
33	45.8	.04	.33	7.7	1.9	9.6	18.4	2.4	20.8
38	53.7	.10	.71	5.0	4.6	9.6	16.4	6.7	23.1
80	76.0	.05	.30	7.8	2.6	10.4	27.0	4.3	31.3
72	89.3	.08	.35	8.8	3.5	12.3	20.5	5.5	26.0
15	62.0	.36	1.47	5.9	9.8	15.7	20.9	14.5	35.4
14	66.7	.06	.22	8.7	1.5	10.2	16.0	1.7	17.7
22	71.9	.07	.36	9.7	2.4	12.1	21.4	2.9	24.3
78	83.7	.06	.31	5.8	2.3	8.1	24.8	4.5	29.3
18	70.7	.11	.76	7.2	4.6	11.8	21.9	6.6	28.5
16	85.6	.07	.33	7.2	2.3	9.5	24.0	2.7	26.7
8	72.5	.06	.34	12.9	1.9	14.8	42.2	2.4	44.6
25	82.9	.07	.37	7.0	2.1	9.1	25.2	2.5	27.7
23	88.7	.26	.91	6.3	5.6	11.9	18.4	7.8	26.2
1	88.3	.16	.73	8.2	3.9	12.1	23.2	4.9	28.1
10	79.4	.04	.21	13.2	1.0	14.2	27.6	1.2	28.8
3	87.9	.08	.37	11.2	1.8	13.0	27.6	2.2	29.8
20	102.8	.11	.40	8.9	2.0	10.9	21.9	2.4	24.3
7	92.4	.08	.33	7.2	1.4	8.6	58.2	1.8	60.0
24	114.0	.13	.40	5.6	2.0	7.6	23.7	3.0	26.7
6	126.2	[1] 1.60	3.77	7.5	16.0	23.5	24.0	20.1	44.1

[1] This soil was leached before determining the wilting percentages.

The frequency diagrams in figure 7 summarize the moisture-retention data at the two wilting values. It is seen that first permanent wilting for these soils occurred in the tension range 5 to 13 atmospheres, with 14 out of the 24 soils wilting in the 7- to 9-atmosphere range. When osmotic effects are added to soil-moisture tension it is seen that at first permanent wilting these soils are distributed fairly

[10] MAGISTAD, O. C., AYERS, A. D., WADLEIGH, C. H., and GAUCH, H. G. EFFECT OF SALT CONCENTRATION, KIND OF SALT, AND CLIMATE ON PLANT GROWTH IN SAND CULTURES. Plant Physiol. 18: 151–166. 1944.

[11] This calculation is only an approximation, since it involves the assumption that the total dissolved solids and the degree of ionization remain unchanged as the plants dry the soil from the initial extractons percentage to the wilting points. Also the factor 28.5 is not constant but depends on the composition of the salts present.

uniformly over the equivalent pressure range from 7.5 to 16 atmospheres.

Ultimate wilting occurs over a much wider tension range than first permanent wilting. The soil-moisture tension at ultimate wilting was below 30 atmospheres for all but 3 of the soils, and 17 out of the

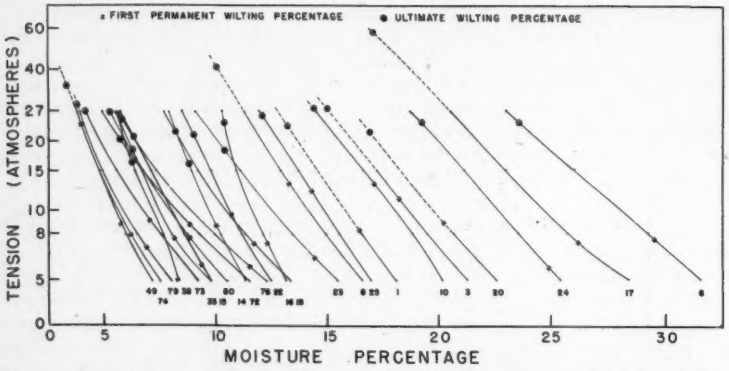

FIGURE 6.—Moisture-retention curves in the wilting range as determined with pressure-membrane apparatus. The ultimate and first permanent wilting percentage points provide an indirect indication of the range in tension.

24 soils underwent permanent wilting in the tension range from 20 to 30 atmospheres. Combining osmotic pressure with soil-moisture tension at ultimate wilting causes no significant rearrangement or grouping of the points in the frequency diagram.

One conclusion that might be drawn from figure 7 is that the phenomena of first permanent and ultimate wilting occur over a range in

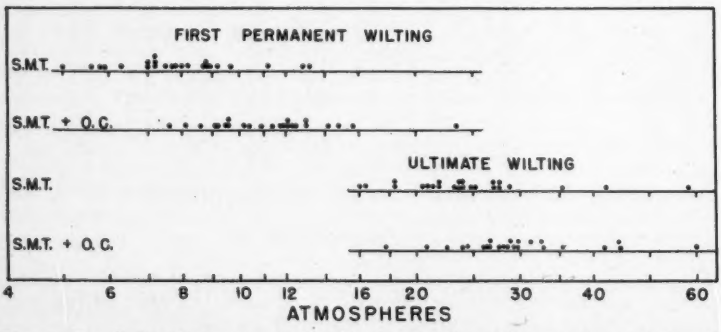

FIGURE 7.—Soil-moisture tension and sum of soil-moisture tension and osmotic concentration at first permanent wilting and ultimate wilting.

tension or free energy. Unfortunately these results must be regarded as tentative, because the moisture-retention curves in figure 6 were determined when many of the soil samples were nearly exhausted from subsampling by different people, and it is possible that the final samples were not entirely representative of the original samples in which the sunflowers were grown.

MOISTURE MOVEMENT IN THE WILTING RANGE

The pressure-membrane apparatus appears to provide a useful means for studying moisture movement in relatively dry soils. The curves in figure 8 show typical summation extraction data from which the curves in figure 6 were determined. The zero of the water-extracted scale was taken at the 5-atmosphere equilibrium, and to conserve space in graphing the curves were returned to the zero of the time scale at each pressure increment. The extraction pressures are indicated on the curves.

A burette clamp was used to mount an ordinary 100-ml. stopcock burette on one of the tripod legs of the extraction cell, and the ex-

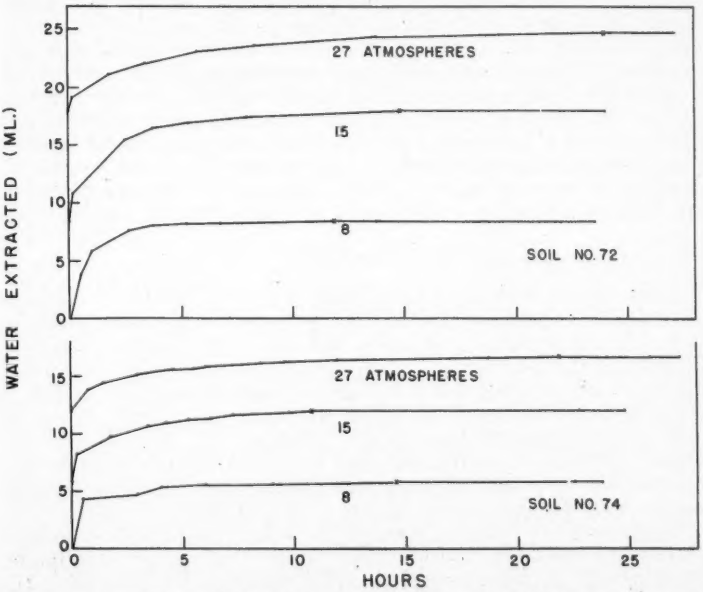

FIGURE 8.—Summation extraction data for two soils, indicating rate of water movement in the 5- to 27-atmosphere tension range. The data were obtained from 400 gm. of soil on a Visking membrane having an area of 660 cm.²

tracted solution was led to the burette tip through a 0.16-mm.-bore copper tube which was closely coupled with rubber tubing. With this arrangement, the gas diffusing through the membrane keeps the extracted solution transported to the burette and a solution outflow of 0.10 ml. or less is easily detectable. The cross on each curve indicates the burette reading at which equilibrium was attained and beyond which no further outflow took place. It is significant that when the 15-atmosphere equilibrium was attained no further outflow took place during a 10- to 15-hour period, but when the extraction pressure was stepped up to 27 atmospheres outflow immediately commenced and continued until a new equilibrium was reached.

There is no indication that 27 atmospheres is anywhere near the limit for this type of experiment either for the satisfactory operation

of the membrane or the moisture-transmitting properties of the soil. Moisture extraction through a Visking membrane has been continued at 15 atmospheres for periods as long as a month with no apparent weakening of the membrane or development of leaks. There is a steady diffusion of gas through the membrane during extraction, and this diffusion rate for nitrogen is approximately 1.3×10^{-6} ml. cm.$^{-2}$ sec.$^{-1}$ atmos.$^{-1}$. Apparently iron rust has a decidedly deteriorating effect on the membrane and will cause leaks in a short time. Trouble from this source can be prevented by a protective coating on the cylinder of the extraction cell.

On the basis of experiments by Lewis (*10*), it is inferred that moisture movement of the type illustrated in figure 8 is over the surface of the soil and that vapor transfer plays a minor role in the absence of temperature gradients.

The statement is repeatedly made in the literature that moisture movement in unsaturated soil ceases at some moisture content not far below the field capacity. This is substantially true for practical purposes when dealing with such problems as the motion of a 12-inch irrigation into a 6-foot layer of dry soil, but one would hesitate to say that moisture movement of the magnitude shown by the 27-atmosphere curves in figure 8 is of no practical importance in time of drought to plants with established root systems.

SOIL-MOISTURE ENERGY RELATIONS

Various means have been used in the past [12] (*4*, *17*) for expressing the energy of retention of water by soil, or the physical condition of water in soil at various moisture contents. The work involved per unit mass in the transfer of a small element of water between a reference state such as a free flat water surface and the moisture system in soil can be expressed in terms of the thermodynamic function partial molal or partial specific free energy. Edlefsen (*7*) and Edlefsen and Anderson (*8*) have recently discussed this function and its usefulness in connection with soil moisture and plant work. Various physical processes and mechanisms contribute to the retention of water by soil, but the free-energy function seems to be suitable for the most general treatment of soil-moisture problems from the energy standpoint. Unfortunately, convenient and accurate methods for measuring the free energy of soil moisture over the plant-growth moisture range are not now available. Vapor-pressure methods do not yet have sufficient precision. Free-energy determinations from freezing-point depression measurements have been made with some success by Schofield and Botelho da Costa (*18*), Bodman and Day (*1*), and Edlefsen and Anderson (*8*), but results appear to depend on the experimental procedure used and difficulties are encountered at moisture contents in the wilting range. As improvements in measuring methods are made (*19*), it is likely that correct use of the theory in calculating the free energy of soil water from freezing-point data will become easier.

On the basis of experimental results obtainable with pressure-membrane apparatus, it is convenient to divide the forces contributing to the energy of retention of moisture by soil into two classes: (1)

[12] DAY, P. R. THE MOISTURE POTENTIAL OF SOILS BY THE CRYOSCOPIC METHOD. 132 pp. 1940. [Thesis on file at Univ. Calif., Berkeley, Calif.]

Those arising from dissolved materials as expressed in terms of osmotic concentration of an extracted sample of the soil solution and (2) all other forces. Force action of the second class can be measured by the use of membranes permeable to the soil solution. The physical quality that is determined experimentally by such membranes is the negative pressure to which a solution must be subjected to be at equilibrium through the membrane with the same solution in the soil.

Past discussions of soil-moisture energy relations have often been confused or ambiguous in their handling of osmotic effects. In spite of its historical significance, the usefulness of capillary potential is considerably lessened by its indefiniteness and by the fact that it is sometimes used as including and sometimes as excluding osmotic effects. It is clear that soil-moisture retention data obtained with tensiometer, suction-plate, pressure-membrane, or centrifugation apparatus are independent of and do not involve solution concentration effects except insofar as the presence of soluble material changes such physical properties of the system as surface tension and density of the soil solution or hydration and flocculation of the soil colloid. Schofield (*17*), in a fruitful and stimulating paper, proposed the pF as a free-energy scale, specifying vapor-pressure and freezing-point methods for its determination. But in the same paper he expressed suction-plate and centrifugation data in terms of pF, thereby neglecting without comment the effect of soluble salts on pF. Many other writers have perpetuated this error in the literature (*9*, *15*, *21*).

If pF is to be accepted as a free-energy scale it should be correctly used and should be clearly distinguished from pressure deficiency or soil-moisture tension. In leached soils, of course, the osmotic component of the pF can be negligible, but in normal soils from semiarid or irrigated regions, dissolved material may account for the major part of the free energy of the soil water. For example, Botelho da Costa (*2*) measured freezing points for 14 California soils supplied by Veihmeyer and found that the average pF at the moisture equivalent was 3.07. Day, [13] using a different freezing-point technique on another set of 14 California soils, found the average value of the pF at the moisture equivalent to be 2.97. If osmotic effects are disregarded, the calculation of tension values from these pF values gives 1,175 and 987 cm. of water, whereas both theoretical and experimental results in a preceding section of this paper indicate that the soil-moisture tension at a moisture percentage equal to the moisture equivalent will account for less than half of these energy values.

At this laboratory, where the effects of salt on the growth and yield of plants are being studied, attempts are being made to segregate and evaluate the effects of soil-moisture tension and osmotic concentration as they operate to determine the availability of moisture to plants. Apparently, considerable work must be done before the energetics of wilting will be well understood, because at present, information on salt effects related to this phenomenon are fragmentary and conflicting.

There is a simple but significant experiment that seems to have a direct bearing on the relation of salt to moisture movement in soil. If a tensiometer is filled with distilled water and the manometer is allowed to attain an equilibrium reading with the porous cup standing in distilled water at a fixed level above the porous surface, it is found

[13] See footnote 12, p. 232

that the manometer indicates practically no change in pressure (less than 0.003 atmosphere) when saturated sodium chloride or other strong salt solution is substituted for the distilled water surrounding the cup. From this it is inferred that in soils in the absence of semipermeable membranes, moisture flow is produced primarily by gravity and gradients in soil-moisture tension and not directly by solution concentration gradients. The semipermeable characteristic of the plant root with its discriminating action against the uptake of most of the common salts must cause a build-up of the salt concentration at the root surface during moisture absorption, and it is possible that a correct appraisal of the root environment with regard to osmotic effects may be even more difficult than with respect to soil-moisture tension.

SUMMARY

By means of porous ceramic and cellulose membranes, a study of soil-moisture retention has been made on samples of 71 southern California soils for which Furr and Reeves determined the moisture equivalent, the first permanent wilting percentage, and the ultimate wilting percentage.

It was found that for 64 of the 71 soils studied the 15-atmosphere percentage lies in the wilting range somewhere between the first permanent wilting percentage and the ultimate wilting percentage. The soil-moisture tension at first permanent wilting for sunflowers was found to range from 5 to 13 atmospheres, but the majority of the soils showed first permanent wilting in the 7- to 9-atmosphere range. The soil-moisture tension at ultimate wilting was below 30 atmospheres for all but 3 of the soils, and 17 out of the 24 soils tested underwent permanent wilting in the range from 20 to 30 atmospheres. Moisture transfer in soils at moisture contents in the wilting range, as indicated by the rate of extraction of moisture from soil in the pressure-membrane apparatus at 15 and 27 atmospheres, is apparently more rapid than can be accounted for by vapor diffusion and should be of practical importance to plant-root systems under drought conditions.

The moisture equivalent is the average value over approximately the 0.1- to 1.0-atmosphere tension range for a moisture retention curve that takes into account centrifuge packing effects. From determinations made on a suction plate it was found that, on an average for the 71 soils studied, the moisture retained by an air-dried and screened but uncentrifuged sample at a tension of one-third of an atmosphere corresponds closely to the moisture equivalent. A set of moisture-retention curves, covering the tension range from 2 to 20,000 cm. of water and for a wide range of soil textures, shows considerable intercrossing of the various curves throughout the whole tension range.

Tensiometer, suction-plate, pressure-plate, pressure-membrane, or centrifugation apparatus may be used for determining equivalent negative pressure or soil-moisture tension, but, without disregarding osmotic effects, none of these can be used for determining pF if the latter is to be taken as a free-energy scale as originally proposed.

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DEFICIENCY, TOXICITY, AND ACCUMULATION OF BORON IN PLANTS [1]

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INTRODUCTION

In some irrigated areas of the West, the concentration of boron in the water supply is so high as to cause injury to field and dooryard plantings, whereas in other areas the concentration is so low as to suggest that here and there boron applications might improve the growth of plants with high boron requirements.

The symptoms of boron deficiency and boron excess are often so striking in character that they are of great value in the interpretation of the boron conditions existing on irrigated lands as well as on agricultural lands generally. The symptoms of deficiency and injury show so much variation, however, between species in respect both to character and intensity, that background information of definite nature is almost a requisite to satisfactory diagnosis or reliable conclusions.

The work on which this paper is based was begun in 1929. Since the work was completed, much has been published on the morphological changes and physiological reactions induced by a lack or an excess of boron, together with other results on many of the plants included herein. Inasmuch as all or nearly all of this literature has found a place in comprehensive abstracts, it has not seemed necessary to review it here.

The present paper reports the results of tests to determine the symptoms, growth reactions, and boron-accumulation characteristics of plants grown in sand cultures supplied with different quantities of boron.

MATERIAL AND METHODS

MATERIAL

Fifty species of plants (58 varieties) were grown out of doors in each of 6 large sand cultures. These cultures were supplied with nutrient solutions containing a trace (0.03 to 0.04 p. p. m.), 1, 5, 10, 15, and 25 parts per million of boron, respectively. When the tolerance

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of the plants and other conditions of the experiment permitted, the plantings were carried to an advanced stage of maturity. The weights of the plants produced and the concentrations of boron in the leaves and other parts were determined. The inclusion of so large a number of species in the work limited the number of plants of each that could be grown and, owing to the small populations, it was necessary to select carefully the plants for transplanting or to plant many extra seeds so that offtype, especially vigorous, or undersized individuals could be discarded during the successive stages of thinning.

The investigation was conducted at Riverside, Calif., and the data reported were obtained during the period from May 1930 to March 1934. There were four summer and four winter plantings, each of which included six or more varieties grown together in each of the sand cultures.

PLAN OF PROCEDURE

The investigation was begun on an exploratory basis in 1929 with five sand beds. The summer and winter plantings of that year provided an opportunity for orientation not only in regard to the diversity and nature of the boron reactions of plants but also for the improvement of experimental procedure. Although the 1929 data are not tabulated in this paper, they are regarded as valid and are occasionally referred to for additional information on crops grown during the succeeding years.

The 1929 results served to emphasize the diversity in the boron requirements and tolerance of different species and indicated that six boron concentrations probably represented the minimum number of treatments that could reasonably be expected to serve the purposes of the investigation. Accordingly, it became necessary to evaluate the advantages, on the one hand, of using fewer concentrations of boron in the interest of replicated treatments and the customary criteria of statistical significance or, on the other hand, of using the six concentrations and relying on departures from the growth and boron-accumulation trends and on the development of plant symptoms through the series of successively higher concentrations as observational indications of plant variability and significance. The latter course was followed.

Substantial diversity was found in the growth and boron-accumulation characteristics of plants included in more than one experiment. Inasmuch as the same methods were followed throughout the work, it has seemed most reasonable to associate such differences in behavior with differences in weather conditions. The weather data presented in table 1 (p. 243) cover the last half of the growth period of each crop and include the average daily maximum temperature, relative humidity at 12 noon, evaporation per week from a standard 4-foot tank, and hours of sunshine, all of which are stated as weekly averages taken to the nearest Monday from the records of the Citrus Experiment Station Riverside, Calif. In its influence on the boron concentrations in the plants at time of harvest, the weather during the final half of the growth period has, beyond reasonable doubt, a greater significance than that of the full period. The early growth rate may often go far in determining ultimate plant size, but it is usually true that more than half of the total carbon assimilation occurs during the final half of the period of growth.

In these experiments growth was always conditioned to some extent by the proximity of the plants to neighboring plants. Excessive exposure was regarded as nontypical of field conditions, and for that reason an effort was made in arranging and spacing the plantings to anticipate the magnitude of the subsequent growth so that neither shading nor exposure would be excessive; unavoidably there were departures from the conditions regarded as ideal. Because of their curtailed growth the high-boron plants, in nearly all instances, were more exposed to light and wind than the low-boron plants; but this effect, while probably altering some of the plant reactions, was not regarded as especially undesirable from an agronomic viewpoint, inasmuch as similar relations exist in field plantings. The spacing and order of planting were always the same in all of the treatments of any experiment.

The base nutrient employed proved to be well suited to the purpose of the experiment and supported a creditable growth of all plants, but it does not follow that it was the most favorable solution possible for any one of the plants or that it was equally suitable during the successive stages of plant development. This particular culture solution would not have been satisfactory had the hydrogen-ion concentrations been controlled at a pH value as low as 6, for example, since in such cases higher concentrations of phosphate would have remained in solution and iron chlorosis would have resulted in at least some of the species.

As a rule the boron determinations on the plant material were not run in duplicate; to have done so would have made it necessary to omit many of the analyses of the different plant parts. The method employed for the determination of boron in plant material has customarily been found to be accurate to within 10 or 15 p. p. m., but throughout the data there are indications that errors of greater magnitude sometimes occurred. In the interpretation of the boron measurements, as was indicated in the instance of plant weights, a measure of emphasis can properly be placed on the trends through the successive six treatments.

Boron accumulates in leaves as they age, and leaf abscission in a number of plants is one of the most noticeable effects of excess accumulation. This fact made it necessary to decide in advance whether it would be better to save leaves as they fell from plants, including them in the total weight and in the samples for analyses, or to let the intact portion of the plant and its boron content at time of harvest stand as the criterion of effect of the treatment. The latter course was followed, but the loss of old leaves high in boron unquestionably resulted in many instances in lower concentrations than would have been found if all dead leaves had been saved.

METHODS

The outdoor sand-culture equipment (*5*)[4] is illustrated in figure 1, which shows the crops and sand beds in July 1933. Except as noted in the tables, the seeds were planted directly in the sand and supplied from the start with culture solutions containing the designated concentrations of boron. The sand in these beds retained approximately 140 liters of solution against gravity. The solution retained by the

[4] Italic numbers in parentheses refer to Literature Cited, p. 277.

sand was displaced once or twice each day by flooding the surface of the sand beds with 180 liters of solution. The displaced solutions drained into auxiliary reservoirs, where they were made up to volume, by the addition of water, for reuse. As soon as the plants in any experiment had become well established, new solutions (180 liters) were systematically substituted for those in use, at intervals customarily of 5 to 15 days, depending on the amount of vegetation in the beds and the climatic conditions.

Throughout the experiment the new base nutrient solution for all treatments was made up with 6, 3, and 3 millimoles per liter, respectively, of calcium nitrate, magnesium sulfate, and monopotassium

FIGURE 1.—Sand cultures in July 1933.

phosphate. Manganese was added to produce a concentration of 0.5 p. p. m., and iron tartrate was supplied as needed. Traces of zinc were derived from the chemicals in the culture solution and from the galvanized pipes. Distilled water was used for making up and replenishing the culture solutions in the trace-boron bed, and tap water was used for the others.

Occasionally complete analyses were made of the used solutions. None of these analyses indicated that any of the constituents of the base nutrient were ever sufficiently low to retard growth. An extensive precipitation of calcium phosphate occurred when the new solutions were mixed with the more alkaline residual solutions retained in the sand, and further precipitation occurred as the hydrogen-ion concentrations decreased with the use of solutions. As a consequence of this precipitation, the concentration of HPO_4 ion actually present in the solutions in the sand during the short cycles between solution changes varied from about 0.4 to 0.1 milliequivalent per liter.

Measurements of hydrogen-ion concentrations were made on all new and discarded solutions. The pH values of the new solutions before passage through the sand, with few exceptions, were in the 6.3 to 6.5 range, and those of the used solutions, at the time of discarding, were in the 6.9 to 7.7 range, values between 7.3 and 7.5 being the most typical.

The boron determinations on both plant materials and culture solutions were made by methods described by Wilcox (*14*, *15*). The average of 31 boron determinations made on new trace-boron solutions was 0.03 p. p. m., and the average of 40 determinations on solutions as discarded was 0.04 p. p. m. The lowest concentration found was an undeterminable trace and the highest was 0.11 p. p. m. The analyses showed no evidence of significant differences in the boron concentrations of the solutions used for the successive plantings.

In harvesting the plants it was customary to flush the beds with solution and, while the sand was saturated or nearly so, to pull out the roots. These pulled roots are included as a part of the entire plant weight unless otherwise indicated.

EXPERIMENTAL RESULTS

PLANTS INCLUDED IN SURVEY

The data on the growth reactions and the boron-accumulation characteristics of the plants included in the investigation are reported in table 1, in the order of the relative tolerance of the plants to boron. These plants and their position by number in table 1 are as follows:

Alfalfa (47–49), artichoke (71), asparagus (72), barley (20), blackberry (1), cabbage (35), calendula (38), California-poppy (56), carrot (28, 29), celery (44), cherry (4), common beet (58, 59), corn (32, 33), cotton (70), cowpea (16), elm (3), fig (7), grape (10, 11), Jerusalem-artichoke (17), Kentucky bluegrass (31), kidney bean (14, 15), larkspur (18), leaf beet (60), lemon (2), lettuce (50, 51), lima bean (23), lupine (9), milo (36, 37), muskmelon (61), mustard (45), oats (43), onion (25–27), oxalis (69), pansy (13), parsley (46), pea (21, 22), peach (5), persimmon (6), potato (34), radish (39–42), redpepper (30), strawberry (8), sugar beet (65–68), sweetclover (62, 63), sweet pea (64), sweetpotato (24), tobacco (52), tomato (54,55), turnip (57), vetch (53), violet (12), and zinnia (19).

TABLE 1.—*Boron accumulation in various plants and its effect*

BORON-SENSITIVE

No.	Crop: Name	Crop: Variety and description	Crop: Date planted	Crop: Date cropped	Plants cropped	Boron deficiency symptoms with trace boron [1]	Boron concentration for best growth [2]	Relative tolerance [3]	Lowest concentration for injury [4]	Part weighed
					No.		*P. p. m.*	*Pct.*	*P. p. m.*	
1	Blackberry (*Rubus* sp.).	Mammoth Thornless.	Apr.	Nov.	1	S	Trace	....	1	All.
2	Lemon (*Citrus limonia* Osbeck).	Eureka, cuttings rooted in December (4 plants).	May	Sept.	1	None	Trace	....	1	do.
3	Elm (*Ulmus americana* L.).	American, selected 12-inch seedlings.	Apr.	Nov.	1	S	1	....	1	do.
4	Cherry (*Prunus avium* L.).	Mazzard, seedlings from previous year (3 plants).	Apr.	Nov.	1	S	1	....	5	do.
5	Peach (*Prunus persica* (L.) Batsch).	Seedlings from previous year (2 plants).	Apr.	Nov.	2	None	1	....	5	do.
6	Persimmon (*Diospyros kaki* L., f.).	Kaki, seedlings from previous year cut back (3 plants).	Apr.	Nov.	1	S	1	....	1	do.
7	Fig (*Ficus carica* L.).	Kadota, year-old cuttings with tops and roots cut back (2 plants).	Apr.	Nov.	1	S	1	....	5	do.
8	Strawberry (*Fragaria* sp.).	Klondike (3 plants).	Nov.	Mar.	3	None	1	....	5	do.
9	Lupine (*Lupinus hartwegi* Lindl.).	Hartweg (5 plants).	Oct.	Apr.	5	M	1	....	5	do.
10	Grape (*Vitis vinifera* L.).	Malaga, single year-old plant cut back.	Apr.	Nov.	1	S	1	9	5	do.
11	do.	Sultanina, single year-old plant cut back.	May	Sept.	....	S	1	....	5	All (green).
12	Violet (*Viola odorata* L.).	Princess of Wales (4 transplants).	Oct.	Mar.	4	None	Trace	20	5	All.
13	Pansy (*Viola tricolor* L.).	5 small transplants.	Oct.	Mar.	5	None	Trace	24	5	do.

See footnotes at end of table.

on growth, with other symptoms, under different climatic conditions

PLANTS

Dry weight[5] of plants grown in solution with indicated concentration of boron (p. p. m.)						Part analyzed	Boron in plants[6] grown in solution with indicated concentration of boron (p. p. m.)						Average climaitc conditions during last half of growth period			
Trace	1	5	10	15	25		Trace	1	5	10	15	25	Maximum temperature	Relative humidity	Evaporation per week	Sunshine
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*°F.*	*Pct.*	*In.*	*Hr.*
145	137	10	----	----	----	Leaves	9	210	717	----	----	----	82.9	69.3	1.42	9.1
						Stems	12	18	----	----	----	----				
						Roots	16	68	----	----	----	----				
						Weighted mean.[7]	11	122	----	----	----	----				
47	27	11	----	----	----	Leaves	61	314	1,232	----	----	----	97.3	70.0	1.91	11.0
						Other parts	11	33	54	----	----	----				
						Weighted mean.	34	147	589	----	----	----				
145	150	27	----	----	----	Leaves	27	277	943	----	----	----	89.6	68.5	1.45	9.2
						Stems	13	14	22	----	----	----				
						Roots	18	35	43	----	----	----				
						Weighted mean.	18	103	197	----	----	----				
61	63	16	----	----	----	Leaves	14	104	182	----	----	----	89.6	68.5	1.45	9.2
						Stems	2	23	85	----	----	----				
						Roots	2	54	----	----	----	----				
						Weighted mean.	6	49	----	----	----	----				
363	396	172	----	----	----	Leaves	17	81	170	----	----	----	89.6	68.5	1.45	9.2
						Stems	7	44	138	----	----	----				
						Roots	2	53	192	----	----	----				
						Weighted mean.	8	57	160	----	----	----				
64	71	36	10	----	----	Leaves	40	389	1,182	----	----	----	89.9	68.5	1.45	9.2
						Stems	31	22	28	56	----	----				
						Roots	8	46	77	163	----	----				
						Weighted mean.	28	132	362	----	----	----				
169	455	138	10	----	----	Leaves	15	404	722	1,296	----	----	89.6	68.5	1.45	9.2
						Roots	10	28	63	----	----	----				
11	12	4	4	3	----	All	44	113	315	450	755	----	75.8	67.1	.79	6.2
57	79	11	4	----	----	do	27	96	367	815	----	----	68.6	66.0	.91	7.5
150	379	74	18	15	----	Leaves	38	250	926	1,774	----	----	89.2	69.3	1.42	9.1
						Stems	28	50	50	155	----	----				
383	720	145	125	----	----	Leaves	86	267	1,804	----	----	----	97.3	70.0	1.91	11.0
35	34	14	5	2	----	All	13	49	153	274	262	----	64.0	69.8	.73	6.9
75	47	33	17	4	----	do	16	59	275	504	822	----	74.8	62.5	.78	6.6

TABLE 1.—*Boron accumulation in various plants and its effect on growth,*

No.	Crop: Name	Crop: Variety and description	Crop: Date planted	Crop: Date cropped	Plants cropped	Boron deficiency symptoms with trace boron [1]	Boron concentration for best growth [2]	Relative tolerance [3]	Lowest concentration for injury [4]	Part weighed
					No.		*P. p. m.*	*Pct.*	*P. p. m.*	
	BORON-SENSITIVE									
14	Kidney bean (*Phaseolus vulgaris* L.).	Navy (5 plants)	May	Sept.	5	None	1		1	All
15	do	Navy (8 plants)	June	Aug.	8	D	Trace	32	1	do
16	Cowpea (*Vigna sinensis* (Torner) Savi).	Whippoorwill (8 plants).	June	Aug.	8	D	Trace	30	5	do
17	Jerusalem-artichoke (*Helianthus tuberosus* L.).	From tubers (8 plants).	Apr.	July	8	None	1	34	1	do
18	Larkspur (*Delphinium* sp.).		Oct.	Mar.	11	S	1	43	5	do
19	Zinnia (*Zinnia elegans* Jacq.).	Yellow (7 plants)	May	Sept.	7	None	Trace	45	1	do
	BORON-SEMI-									
20	Barley (*Hordeum vulgare* L.).	California Common Coast, cropped when partly ripe (21 plants).	Apr.	July	21	D	Trace	51	5	Grain Other Total
21	Pea (*Pisum sativum* L.).	Hundredfold (5 plants).	Dec.	May	5	None	1	55	5	All
22	do	American Wonder (5 plants).	Oct.	Mar.	5		1	53	1	do
23	Lima bean (*Phaseolus lunatus* L.).	Burpee Bush (5 plants).	May	Sept.	5	S	Trace	57	1	do
24	Sweetpotato (*Ipomoea batatas* (L.) Lam.).	(2 plants)	June	Oct.	2	S	Trace	63	5	Tops Roots Total
25	Onion (*Allium cepa* L.).	Riverside Sweet Spanish (7 plants in 10-boron, 12 elsewhere).	Dec.	Apr.	12	None	Trace	68	1	Leaves Roots Total
26	do	Riverside Sweet Spanish (6 plants cropped early).	May	July	6	None	Trace	75	1	Leaves Roots Total

See footnotes at end of table.

with other symptoms, under different climatic conditions—Continued

PLANTS—Continued

Dry weight[5] of plants grown in solution with indicated concentration of boron (p. p. m.)						Part analyzed	Boron in plants[6] grown in solution with indicated concentration of boron (p. p. m.)						Average climatic conditions during last half of growth period			
Trace	1	5	10	15	25		Trace	1	5	10	15	25	Maximum temperature	Relative humidity	Evaporation per week	Sunshine
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	°*F.*	*Pct.*	*In.*	*Hr.*
322	401	210	5	-----	-----	All	12	191	648	645	-----	-----	96.5	68.5	2.03	10.1
628	583	376	189	39	-----	Leaves	Trace	151	690	1,254	1,733	-----	96.6	66.0	1.94	11.5
						Other	11	27	41	89	138	-----				
						Weighted mean.	6	85	359	705	997	-----				
422	332	259	101	19	-----	Leaves	32	119	404	722	1,132	-----	96.6	66.0	1.94	11.5
						Other	22	30	59	99	167	-----				
						Weighted mean.	27	70	195	296	573	-----				
628	640	372	189	93	-----	Dead leaves	171	519	986	1,550	1,590	-----	87.4	69.0	1.28	6.7
						Other	27	92	221	353	427	-----				
						Weighted mean.	28	98	377	746	1,001	-----				
110	168	114	75	29	14	All	124	110	286	602	918	820	73.9	62.2	.73	6.5
693	648	439	330	158	19	Leaves	90	436	1,241	2,191	2,739	3,080	98.1	68.3	2.05	11.2
						Other	41	76	95	220	237	429				
						Weighted mean.	54	183	424	859	1,187	1,685				
TOLERANT PLANTS																
102	90	65	64	21	19	Grain	3	11	12	27	45	51	88.7	69.0	1.44	7.9
283	238	169	154	112	71	Other	19	104	299	652	953	1,395				
385	328	234	218	133	90	Weighted mean.	15	78	219	469	810	1,111				
195	203	121	105	109	64	Leaves	16	212	609	-----	1,283	1,452	72.5	66.8	.91	8.0
						All	16	64	230	338	436	562				
31	36	26	24	8	5	----do	56	110	319	364	435	867	64.7	71.7	.81	6.8
154	----	100	92	70	1	----do	26	206	515	1,181	1,298	-----	94.3	70.3	1.91	9.9
815	722	698	553	335	73	Tops	16	118	310	602	894	1,410	91.4	69.7	1.21	9.0
358	262	276	278	80	24	Roots	6	44	20	33	88	90				
1,173	984	974	831	415	97	Weighted mean.	13	98	228	412	739	1,083				
21	15	16	13	17	15	Leaves	30	104	270	520	987	1,578	78.0	70.3	1.28	9.5
12	8	8	5	8	7	Roots	23	36	105	150	325	346				
33	23	24	18	25	22	Weighted mean.	27	80	215	417	775	1,186				
9	7	5	7	7	6	Leaves	29	115	354	530	876	1,488	95.0	66.3	2.04	12.2
7	6	5	6	6	3	Roots	-----	21	54	64	84	119				
16	13	10	13	13	9	Weighted mean.	-----	72	204	315	510	1,032				

TABLE 1.—*Boron accumulation in various plants and its effect on growth,*

BORON-SEMI-

Crop					Plants cropped	Boron deficiency symptoms with trace boron [1]	Boron concentration for best growth [2]	Relative tolerance [3]	Lowest concentration for injury [4]	Part weighed
No.	Name	Variety and description	Date planted	Date cropped						
					No.		*P. p. m.*	*Pct.*	*P. p. m.*	
27	Onion (*Allium cepa* L.).	Riverside Sweet Spanish (final 6 plants of crop No. 26).	May	Sept.	6	None	Trace	64	1	Leaves Roots Total
28	Carrot (*Daucus carota* L.).	Danvers Half Long (14 plants).	Dec.	Apr.	14	None	Trace	70	10	Laminae Roots Other Total
29	....do....	....do....	May	Sept.	14	None	Trace	70	5	Laminae Roots Other Total
30	Redpepper (*Capsicum frutescens* L.).	Sweet Chinese Giant (3 plants).	Apr.	Oct.	3	None	Trace	71	5	Leaves Fruit Other Total
31	Kentucky bluegrass (*Poa pratensis* L.).	2 18-inch rows cut in May, cropped in June.	Dec.	May June	....	None None	1 5	73 86	1 1	Leaves All
32	Corn (*Zea mays* L.)	Iowa Yellow Dent (3 plants), cropped before flowering.	Apr.	June	3	None	1	53	5	All
33	....do....	Iowa Yellow Dent (3 plants).	June	Oct.	3	M	5	79	5	Leaves Grain Other Total
34	Potato (*Solanum tuberosum* L.).	British Queen (3 plants; in 10-boron, 4 elsewhere).	Dec.	May	4	S	1	78	1	Leaves Tubers Other Total
35	Cabbage (*Brassica oleracea* var. *capitata* L.).	Early Flat Dutch (3 plants), cropped soon after heading had started.	Dec.	Apr.	3	None	1	78	10	Green laminae. Covered laminae. Other Total
36	Milo (*Sorghum vulgare* Pers.).	Dwarf Yellow (3 plants).	May	Nov.	3	M	Trace	(5)	5	Leaves Heads Roots Other Total

See footnotes at end of table.

with other symptoms, under different climatic conditions—Continued

TOLERANT PLANTS—Continued

Dry weight[5] of plants grown in solution with indicated concentration of boron (p. p. m.)						Part analyzed	Boron in plants[6] grown in solution with indicated concentration of boron (p. p. m.)						Average climatic conditions during last half of growth period			
Trace	1	5	10	15	25		Trace	1	5	10	15	25	Maximum temperature	Relative humidity	Evaporation per week	Sunshine
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*°F.*	*Pct.*	*In.*	*Hr.*
16	8	8	8	8	9	Leaves	44	91	242	510	679	926	98.1	68.3	2.05	11.2
37	23	26	27	24	27	Roots	28	46	46	74	87	155				
53	31	34	35	32	36	Weighted mean.	33	58	92	174	235	348				
33	23	30	22	13	12	Laminae	36	66	124	324	542	788	78.0	70.3	1.28	9.5
59	42	56	32	24	14	Roots	22	33	64	154	231	319				
35	34	43	27	18	15	Other	28	55	55	121	148	174				
127	99	129	81	55	41	Weighted mean.	27	48	75	189	277	403				
53	50	45	37	33	30	Laminae	38	204	395	999	1,165	1,244	97.3	70.0	1.91	11.0
26	24	15	14	13	19	Roots	25	57	65	131	117	114				
55	59	51	37	37	32	Other	38	65	103	181	166	209				
134	133	111	88	83	81	Weighted mean.	35	116	216	517	556	570				
119	107	147	81	63	49	Leaves	34	118	328	700	729	882	92.2	71.0	1.40	9.4
224	218	132	171	109	34	Fruit	-----	21	16	24	34	46				
124	101	150	85	55	53	Other	-----	19	24	31	51	48				
467	426	429	337	227	136	Weighted mean.	-----	45	126	188	231	348				
46	49	45	44	20	13	Leaves	3	22	92	164	224	398	72.5	66.8	.91	8.0
18	21	22	20	11	10	All	8	41	153	361	477	1,185	81.8	64.4	1.52	9.5
422	447	337	245	134	48	do	11	32	123	235	377	727	82.5	70.3	1.41	7.5
186	254	183	169	146	120	Leaves	27	72	179	-----	-----	-----	90.0	73.5	1.05	8.4
390	364	699	417	360	229	-----	-----	-----	-----	-----	-----	-----				
633	734	507	372	368	343	-----	-----	-----	-----	-----	-----	-----				
1,209	1,352	1,689	958	874	692	-----	-----	-----	-----	-----	-----	-----				
139	131	111	145	78	57	Leaves	16	98	399	685	1,311	1,644	72.4	64.8	1.08	8.2
591	796	713	599	490	177	Tubers	8	22	13	41	27	65				
102	92	75	118	55	42	Other	22	32	43	75	99	127				
832	1,019	899	862	623	276	Weighted mean.	11	33	63	154	194	401				
140	234	147	172	174	132	Green laminae	16	104	204	440	561	1,152	78.0	70.3	1.28	9.5
23	17	25	22	24	9	Covered laminae.	22	52	55	60	94	110				
108	163	134	138	127	98	Other	28	52	-----	74	116	176				
271	414	306	332	325	239	Weighted mean.	21	81	-----	263	353	713				
285	131	92	117	108	45	Leaves	16	138	625	1,204	1,461	2,009	88.3	68.0	1.32	9.1
678	492	461	378	275	41	Stalks + sheaths.	11	11	23	61	103	261				
253	61	68	79	49	24	-----	-----	-----	-----	-----	-----	-----				
670	206	235	271	200	71	-----	-----	-----	-----	-----	-----	-----				
1,886	890	856	845	632	181	-----	-----	-----	-----	-----	-----	-----				

TABLE 1.—*Boron accumulation in various plants and its effect on growth.*

BORON-SEMI-

No.	Crop: Name	Crop: Variety and description	Crop: Date planted	Crop: Date cropped	Plants cropped	Boron deficiency symptoms with trace boron [1]	Boron concentration for best growth [2]	Relative tolerance [3]	Lowest concentration for injury [4]	Part weighed
					No.		P. p. m.	Pct.	P. p. m.	
37	Milo (*Sorghum vulgare* Pers.).	Dwarf Yellow (4 plants).	July	Dec.	4	M	1	80	1	Leaves Grain Other Total
38	Calendula (*Calendula officinalis* L.).	Orange King (7 plants).	Dec.	Apr.	7	None	Trace	80	5	Leaves Other Total
39	Radish (*Raphanus sativus* L.).	Early Scarlet (15 plants).	Dec.	Feb.	15	S	1	60	10	Leaves Roots Total
40	do	Early Breakfast (10 plants).	Oct.	Nov.	10	S	Trace	85	10	Leaves Roots Total
41	do	Early Scarlet (15 plants).	Dec.	Mar.	15	S	5	90	10	Leaves Roots Total
42	do	Early Scarlet (20 plants).	June	July	20	None	5	91	10	Leaves Roots Total
43	Oats (*Avena sativa* L.).	Kanota badly lodged and cropped before ripe (21 plants).	Apr.	July	21	None	5	86	5	Grain Other Total
44	Celery (*Apium graveolens* L.).	Seeded in Aug. and transplanted to cultures (5 plants).	Nov.	Mar.	5	S	15	89	25	Leaflets Other Total
45	Mustard (*Brassica* sp.).	Yellow-seeded (5 plants).	Oct.	Jan.	5	None	1	94	10	All
46	Parsley (*Petroselinum crispum* (Mill.) Nym.).	Double Curled (12 plants).	Oct.	Mar.	12	None	5	95	15	do
47	Alfalfa (*Medicago sativa* L.).	Chilean (20 plants were left in each bed when thinned; of these 20, 20, 20, 19, 18, and 11 survived respectively).	Dec.	Apr.	----	None	10	106	15	Leaves Other Total

See footnotes at end of table.

with other symptoms, under different climatic conditions—Continued

TOLERANT PLANTS—Continued

Dry weight[5] of plants grown in solution with indicated concentration of boron (p. p. m.)						Part analyzed	Boron in plants[6] grown in solution with indicated concentration of boron (p. p. m.)						Average climatic conditions during last half of growth period			
Trace	1	5	10	15	25		Trace	1	5	10	15	25	Maximum temperature	Relative humidity	Evaporation per week	Sunshine
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*°F.*	*Pct.*	*In.*	*Hr.*
407	559	409	320	302	201	Leaves + sheaths.	8	24	111	222	292	342	76.8	59.5	.80	7.0
542	543	534	505	292	114	Grain	Trace	Trace	Trace	3	7	13				
890	867	996	719	644	371	Other	Trace	Trace	22	49	70	160				
1,839	1,969	1,939	1,544	1,238	686	Weighted mean.	2	7	35	70	109	189				
70	64	64	46	50	50	Leaves	33	272	715	1,490	1,986	2,106	77.1	71.4	1.24	9.5
123	125	109	100	97	68	Other	11	44	94	110	170	231				
193	189	173	146	147	118	Weighted mean.	19	121	324	545	788	1,025				
19	24	19	14	10	12	Leaves	33	36	58	86	145	209	67.9	75.6	1.03	6.4
9	14	11	7	7	7	Roots	15	20	33	62	58	98				
28	38	30	21	17	19	Weighted mean.	27	30	49	78	109	168				
21	16	19	18	17	10	Leaves	13	55	96	192	197	375	79.0	67.8	.74	7.8
18	16	16	15	14	9	Roots	33	30	49	66	66	116				
39	32	35	33	31	19	Weighted mean.	22	43	75	135	138	254				
33	36	38	39	34	33	Leaves	8	59	155	337	423	714	68.7	64.5	.93	8.0
23	32	31	21	21	13	Roots	24	27	51	99	124	170				
56	68	69	60	55	46	Weighted mean.	15	44	108	254	309	560				
24	28	30	30	21	19	Leaves	24	89	196	407	679	1,151	91.4	69.6	1.44	12.1
20	26	25	22	19	15	Roots	13	30	59	86	127	183				
44	54	55	52	40	34	Weighted mean.	19	61	134	271	417	724				
45	33	64	35	23	9	Grain	13	19	43	107	184	419	88.7	69.0	1.44	7.9
234	280	303	217	167	86	Other	5	69	334	706	1,096	1,748				
279	313	367	252	190	95	Weighted mean.	6	64	283	623	986	1,622				
43	99	80	78	97	54	Leaflets	20	68	140	297	432	720	74.8	67.3	.73	6.0
54	131	94	111	152	99	Other	30	60	118	256	379	734				
97	230	174	189	249	153	Weighted mean.	26	63	128	273	400	729				
443	527	526	460	497	348	All	49	65	80	108	148	205	60.7	69.3	.59	6.0
176	183	214	200	104	3	do	16	43	172	388	588	890	74.8	62.5	.78	6.6
79	70	73	85	77	42	Leaves	28	182	330	627	740	996	78.0	70.3	1.28	9.5
197	209	221	237	195	102	Other	11	14	28	55	52	-----				
276	279	294	322	272	144	Weighted mean.	16	56	103	206	247	-----				

TABLE 1.—*Boron accumulation in various plants and its effect on growth,*

Crop											
No.	Name	Variety and description	Date planted	Date cropped	Plants cropped	Boron deficiency symptoms with trace boron [1]	Boron concentration for best growth [2]	Relative tolerance [3]	Lowest concentration for injury [4]	Part weighed
					No.		*P. p. m.*	*Pct.*	*P. p. m.*	
BORON-SEMI-										
48	Alfalfa (*Medicago sativa* L.).	Chilean (20 plants; many ripened seed when cut).	May	July	20	None	15	98	15	Leaves Stems Total
49	do	Chilean, final cropping; 16, 17, 19, 13, 12, and 10 plants survived in respective beds.	-------	Sept.	----	Mild	5	75	15	Leaves Stems Roots Total
50	Lettuce (*Lactuca sativa* L.).	Los Angeles Market (4 plants).	June	Aug.	4	None	5	96	1	Leaves Other Total
51	do	Big Boston Head (4 plants).	June	Aug.	4	None	5	92	1	Leaves Other Total
52	Tobacco (*Nicotiana tomentosa* Ruiz and Pav.).	Giant Havana Acclimated (3 plants).	May	Aug.	3	None	15	96	10	Laminae Other Total
53	Vetch (*Vicia atropurpurea* Desf.).	Purple (12 plants)	Oct.	Jan.	12	None	5	98	5	All
54	Tomato (*Lycopersicon esculentum* Mill.).	Marglobe, cropped during early fruiting stage (3 plants).	May	July	3	None	10	99	5	Leaves Fruit Other Total
55	do	Stone, cropped early (3 plants).	May	Aug.	3	None	5	94	5	Leaves Other Total
56	California-poppy (*Eschscholtzia californica* Cham.).	7 plants	Dec.	Apr.	7	None	5	99	5	All
BORON-TOLERANT										
57	Turnip (*Brassica rapa* L.).	Purple-top Globe (6 plants, 10-boron plants damaged).	Dec.	May	6	None	5	115	25	Leaves Roots Total
58	Common beet (*Beta vulgaris* L.).	Early Wonder (7 plants).	Dec.	Apr.	7	S(?)	5	112	15	Laminae Roots Other Total

See footnotes at end of table.

with other symptoms, under different climatic conditions—Continued

TOLERANT PLANTS—Continued

Dry weight[5] of plants grown in solution with indicated concentration of boron (p. p. m.)						Part analyzed	Boron in plants[6] grown in solution with indicated concentration of boron (p. p. m.)						Average climatic conditions during last half of growth period			
Trace	1	5	10	15	25		Trace	1	5	10	15	25	Maximum temperature	Relative humidity	Evaporation per week	Sunshine
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*°F.*	*Pct.*	*In.*	*Hr.*
53	60	56	50	70	42	Leaves	39	150	283	410	516	701	97.6	64.2	2.14	12.4
75	73	71	63	81	46	Stems	17	22	17	20	28	39				
128	133	127	113	151	88	Weighted mean.	26	80	134	193	254	355				
13	28	28	17	17	13	Leaves	36	158	388	654	854	859	98.4	70.0	1.84	10.3
18	27	31	21	18	13	Stems	11	31	33	55	94	94				
15	25	22	14	13	6	Roots	31	20	47	47	58	52				
46	80	81	52	48	32	Weighted mean.	25	72	160	249	353	397				
60	49	66	59	58	60	Leaves	27	70	116	221	343	582	96.6	68.0	1.94	11.6
24	18	20	19	20	22	Other	19	24	24	49	61	81				
84	67	86	78	78	82	Weighted mean.	25	58	95	179	271	448				
36	45	44	39	33	35	Leaves	43	75	166	353	459	817	96.6	68.0	1.94	11.6
20	19	22	22	17	22	Other	29	28	27	49	58	86				
56	64	66	61	50	57	Weighted mean.	38	61	120	243	323	535				
124	113	127	114	113	93	Laminae	19	72	261	365	474	771	95.6	67.1	1.74	11.5
221	212	222	194	222	152	Other	24	8	35	27	33	68				
345	325	349	308	335	245	Weighted mean.	22	30	117	152	182	335				
133	129	134	133	125	85	All	73	83	151	208	278	456	60.7	69.3	.47	6.0
106	103	111	122	107	65	Leaves	48	150	544	855	1,192	1,416	94.6	64.4	2.03	12.2
19	16	20	24	20	10	Fruit	24	27	60	79	114	131				
141	129	133	138	113	62	Other	16	27	60	57	68	60				
266	248	264	284	240	137	Weighted mean.	29	78	264	402	573	709				
244	239	367	216	187	185	Leaves	34	103	253	531	684	1,168	97.6	64.8	1.95	11.4
284	335	363	260	232	170	Other	38	32	41	46	63	93				
528	574	730	476	419	355	Weighted mean.	36	62	148	266	340	653				
142	128	171	138	114	93	Leaves	54	108	377	705	822	1,073	77.1	71.4	1.24	9.5
						Other	28	39	64	113	153	186				

PLANTS

206	244	359	-----	271	284	Leaves	16	65	108	-----	213	399	71.9	66.8	0.92	7.7
73	126	110	-----	109	66	Roots	19	38	51	-----	65	132				
279	370	469	-----	380	350	Weighted mean.	17	56	95	-----	171	349				
41	28	35	42	34	33	Laminae	25	104	198	346	671	822	78.0	70.3	1.28	9.5
71	67	94	74	70	69	Roots	-----	16	16	46	74	72				
31	32	50	45	35	33	Other	20	46	50	94	148	165				
143	127	179	161	139	135	Weighted mean.	12	43	61	138	239	278				

TABLE 1.—*Boron accumulation in various plants and its effect on growth,*

BORON-TOLERANT

Crop											
No.	Name	Variety and description	Date planted	Date cropped	Plants cropped	Boron deficiency symptoms with trace boron [1]	Boron concentration for best growth [2]	Relative tolerance [3]	Lowest concentration for injury [4]	Part weighed
					No.		*P. p. m.*	*Pct.*	*P. p. m.*	
59	Common beet (*Beta vulgaris* L.).	Early Wonder (7 plants).	May	Aug.	7	S	10	100	10	Laminae Roots Other Total
60	Leaf beet ((*Beta vulgaris* var. *cicla* L.).	----------	Oct.	Mar.	----	W	5	110	25	All
61	Muskmelon (*Cucumis melo* L.).	4 plants cropped soon after early flowering.	June	Aug.	4	D	5	107	5	Leaves Other Total
62	Sweetclover (*Melilotus indica* (L.) All.).	Annual Yellow (15 plants).	Dec.	Apr.	15	None	5	110	10	Leaves Other Total
63	do	do	May	Aug.	15	None	15	124	10	Leaves Other Total
64	Sweetpea (*Lathyrus odoratus* L.).	8 plants	Dec.	Apr.	8	S	10	113	5	Leaves Seed Other Total
65	Sugar beet (*Beta vulgaris* var. *crassa* Alef.).	B. P. I. 2769 (7 plants).	Dec.	Apr.	7	None	5	121	15	Laminae Roots Other Total
66	do	B. P. I. 2769 (5 plants)	Apr.	Sept.	5	S	5	107	10	Tops Roots Total
67	do	B. P. I. 2769 (7 plants).	May	Sept.	7	S	15	117	10	Laminae Roots Other Total
68	do	U.S. No. 1 (7 plants).	June	Aug.	7	S	10	146	10	Laminae Roots Other Total
69	Oxalis (*Oxalis bowiei* Herb.).	Bowie (5 plants from tubers).	Oct.	Mar.	5	S	10	121	None	All

See footnotes at end of table.

with other symptoms, under different climatic conditions—Continued

PLANTS—Continued

Dry weight[5] of plants grown in solution with indicated concentration of boron (p. p. m.)						Part analyzed	Boron in plants[6] grown in solution with indicated concentration of boron (p. p. m.)						Average climatic conditions during last half of growth period			
Trace	1	5	10	15	25		Trace	1	5	10	15	25	Maximum temperature	Relative humidity	Evaporation per week	Sunshine
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*°F.*	*Pct.*	*In.*	*Hr.*
30	52	43	62	46	54	Laminae	52	150	370	637	986	1,263	99.4	59.4	2.21	12.0
72	124	132	137	113	121	Roots	33	46	46	44	63	82				
22	42	39	49	36	45	Other	35	60	76	74	131	152				
124	218	214	248	195	220	Weighted mean.	38	74	117	198	293	386				
189	254	312	276	248	170	All	16	58	66	82	139	200	64.0	69.8	.73	6.9
63	87	94	89	87	77	Leaves	37	223	923	1,621	2,181	3,875	98.6	64.2	1.96	11.5
47	66	84	72	63	69	Other	16	46	90	163	253	373				
110	153	178	161	150	146	Weighted mean.	28	147	530	969	1,371	2,220				
34	60	79	65	54	64	Leaves	64	214	363	602	1,089	1,438	78.0	70.3	1.28	9.5
64	100	132	97	102	103	Other	6	8	33	38	176	297				
98	160	211	162	156	167	Weighted mean.	26	85	157	264	492	734				
18	21	22	21	30	23	Leaves	58	349	665	1,164	1,597	2,245	99.4	59.4	2.21	12.0
28	31	39	34	47	37	Other	25	36	39	33	47	83				
46	52	61	55	77	60	Weighted mean.	38	162	265	465	651	912				
24	32	35	34	27	26	Leaves	30	190	520	979	1,084	1,551	78.0	70.3	1.28	9.5
5	8	5	4	3	1	Seed	1	18	50	55	----	----				
48	55	73	76	65	74	Other	36	33	74	156	220	352				
77	95	113	114	95	101	Weighted mean.	32	85	211	398	474	664				
43	36	41	43	42	45	Laminae	20	102	143	426	521	668	77.1	71.9	1.24	9.4
44	42	66	65	50	50	Roots	2	6	6	20	31	28				
64	63	81	81	78	67	Other	8	28	58	82	105	166				
151	141	188	189	170	162	Weighted mean.	10	40	58	139	186	263				
39	217	202	183	218	173	Tops	20	89	177	262	304	592	96.5	67.5	2.04	10.2
35	174	242	192	217	207	Roots	6	28	28	38	33	55				
74	391	444	375	435	380	Weighted mean.	13	62	96	147	169	299				
67	106	137	110	152	104	Laminae	35	122	286	612	686	1,008	97.3	70.0	1.91	11.0
51	180	223	151	265	215	Roots	20	13	24	52	22	41				
63	132	153	126	144	148	Other	42	35	46	82	68	133				
181	418	513	387	561	467	Weighted mean.	33	48	101	221	214	286				
41	51	60	77	77	88	Laminae	19	106	234	495	588	975	97.8	63.8	1.76	11.5
40	54	67	93	71	85	Roots	19	27	24	30	38	46				
43	69	86	121	109	107	Other	16	49	49	72	65	88				
124	174	213	291	257	280	Weighted mean.	18	59	93	171	214	354				
99	128	152	165	149	104	All	16	65	264	426	655	1,191	74.8	62.5	.78	6.6

TABLE 1.—*Boron accumulation in various plants and its effect on growth,*

BORON-TOLERANT

Crop											
No.	Name	Variety and description	Date planted	Date cropped	Plants cropped	Boron deficiency symptoms with trace boron [1]	Boron concentration for best growth [2]	Relative tolerance [3]	Lowest concentration for injury [4]	Part weighed
					No.		*P. p. m.*	*Pct.*	*P. p. m.*	
70	Cotton (*Gossypium hirsutum* L.).	Upland, Acala (4 plants).	May	Nov.	4	S	10	130	19	Leaves Green bolls Seed cotton Other Total
71	Artichoke (*Cynara scolymus* L.).	2 plants	Oct.	Mar.	2	S	5	123	5	Laminae Other Total
72	Asparagus (*Asparagus officinalis* L.).	5 seedling transplants; tops cut in October; plants cropped in May.	Apr.	Oct. May	5	S	15	217	25	Tops do Roots Total

[1] S=presence of leaf or other morphological abnormalities; M=time of flowering or ripening substantially affected; D=trace-boron plants more severely attacked by mildew than plus-boron plants; W=severe wilting.

[2] Indicates boron concentration producing greatest total dry weight of plants; the differences between the successively higher concentrations were often small or inconsistent.

[3] Computed by multiplying average weight of plants in 5-, 10-, and 15-boron by 100 and dividing by weight of plants in trace- or 1-boron, whichever of these two was the greater.

SYMPTOMS AND OTHER PLANT REACTIONS

BLACKBERRY (1)[5]—The mesophyll of the leaves in trace-boron was mildly buckled, the terminal buds of the canes had lost their dominance, and by the end of the season numerous short branches had developed near the tips. The older leaves on the 1-boron canes showed slight marginal burning, but otherwise the plants were normal in appearance. Little growth occurred in 5-boron, and the plants in the higher concentrations died early in the season.

LEMON (2).—Deficiency symptoms were absent from trace-boron. The older 1-boron leaves yellowed and burned along the margins; the yellowing extended inward between the veins (pl. 1, *A*). The plants in 5-boron were in very poor condition, and those in 10-, 15-, and 25-boron did not survive.

ELM (3).—Many of the trace-boron elm leaves showed late-season yellowing with occasional dead areas along the margins. Only a few of the 1-boron leaves showed marginal burning, but all 5-boron leaves were severely burned, the necrotic areas extending inward between the veins toward the midrib (pl. 2, *A*).

CHERRY (4).—Leaves that developed on the trace-boron plants during the midsummer months were chlorotic, many of them being green only along the veins, and the marginal serrations were resinous to dead. There were a number of dead leaf tips in 5-boron, but cherry.

[5] Numbers in parentheses refer to table 1.

with other symptoms, under different climatic conditions—Continued

PLANTS—Continued

Dry weight[5] of plants grown in solutions with indicated concentration of boron (p. p. m.)						Part analyzed	Boron in plants[6] grown in solution with indicated concentration of boron (p. p. m.)[7]						Average climatic conditions during last half of growth period			
Trace	1	5	10	15	25		Trace	1	5	10	15	25	Maximum temperature	Relative humidity	Evaporation per week	Sunshine
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*°F.*	*Pct.*	*In.*	*Hr.*
81	113	131	179	111	124	Leaves	16	187	306	522	833	1,625	88.4	69.3	1.34	9.1
16	111	138	199	108	118	Stems & roots	15	24	32	33	48	60				
0	38	20	27	16	32											
107	200	303	367	204	249											
204	462	592	772	439	523											
333	454	510	512	510	423	Laminae	38	112	236	440	830	1,358	73.9	62.2	.73	6.5
282	385	571	482	499	361	Other	16	58	82	66	140	182				
615	839	1,081	994	1,009	784	Weighted mean.	28	87	155	259	489	817				
42	102	183	-----	269	210	Tops	55	74	140	-----	244	288	91.6	69.2	1.39	9.4
14	55	78	-----	163	90	----do	43	54	59	-----	170	175	72.7	65.3	1.02	8.2
22	73	79	-----	226	83	Roots	13	16	30	-----	27	59				
78	230	340	-----	658	383											

[4] First evidence at time of cropping of yellowed or burned leaves, marginal restrictions, or other abnormalities.

[5] Oven-dry weight. [6] Expressed on oven-dry basis.

[7] The boron concentration in each plant part was multiplied by the weight of that part, and the total of these products was divided by the sum of the weights of the plant parts.

[8] Value omitted because of abnormal growth of trace-boron plants.

as observed in other tests, does not show much leaf injury when grown in concentrations of boron sufficiently high to cause growth depression.

PEACH (5).—Deficiency symptoms were lacking in trace-boron of this planting, but in the 1929 experiment the leaves tended to be chlorotic. The 1-boron leaves were normal and the 5-boron leaves appeared so, but the older ones abscised earlier than those in trace-boron and 1-boron. In keeping with observations made in other experiments and in the field, necrotic lesions developed in the 5-boron stem bark. These lesions commonly appear above the leaf axils.

PERSIMMON (6).—The margins of the trace-boron leaves were necrotic to dead. Associated with the relatively high boron accumulation, the leaf margins in 1-boron were cupped downward and yellowed or burned. The 5-boron leaves were severely cupped and burned, yellow areas appearing inward from the margins between the veins (pl. 1, *B*).

FIG (7).—The terminal buds of the trace-boron plants became dormant before the end of the season; there were numerous small branches near the tops of the plants; the successive main-stalk internodes were shorter as the season progressed; the late-season leaves were misshapen, the mesophyll was buckled, and there were large irregular chlorotic and partly dead areas extending inward along the veins from the margins of the leaves. The terminal buds of the 1-boron trees were still growing late in the season, and the leaves and branching habits were normal. All but the upper third of the leaves

in 5-boron were burned along the margins. The average height of plants in trace-, 1-, 5-, and 10-boron was 85, 210, 125, and 11 cm. respectively.

STRAWBERRY (8).—Deficiency symptoms were lacking in the trace-boron plants, and these plants were equal in appearance to those growing in 1-boron. The trace- and 1-boron beds each produced about 20 fruits. When cropped late in March, only a single leaf was alive on each of the 5-boron plants.

LUPINE (9).—There were no deficiency symptoms in the trace-boron plants, but flowering was 3 weeks later than in the 1-boron culture. The leaves on both the 5- and the 10-boron plants were severely burned. All plants in 15- and 25-boron died.

GRAPE (10, 11).—The Malaga grapes grown in 1930 (10) and the Sultanina grapes grown in 1931 (11) reacted similarly. The trace-boron leaves were buckled and had irregular dead areas along the margins. The 1-boron leaves were entirely normal, whereas the 5-boron leaves were reduced in size, the margins were restricted, and there were numerous resinous necrotic patches and spots along the margins. Little of the older leaf tissue of the 10-boron plants was alive at the end of the season. The total length of the Malaga shoots in trace-, 1-, 5-, 10-, and 15-boron was 528, 1,505, 310, 155, and 63 cm. respectively.

VIOLET (12).—There were no deficiency symptoms in trace-boron, the 1-boron plants were likewise normal, the leaves of the 5-boron plants were curled downward at the margins, those of the10-boron were badly burned, and only a few small leaves remained alive in 15-boron until March.

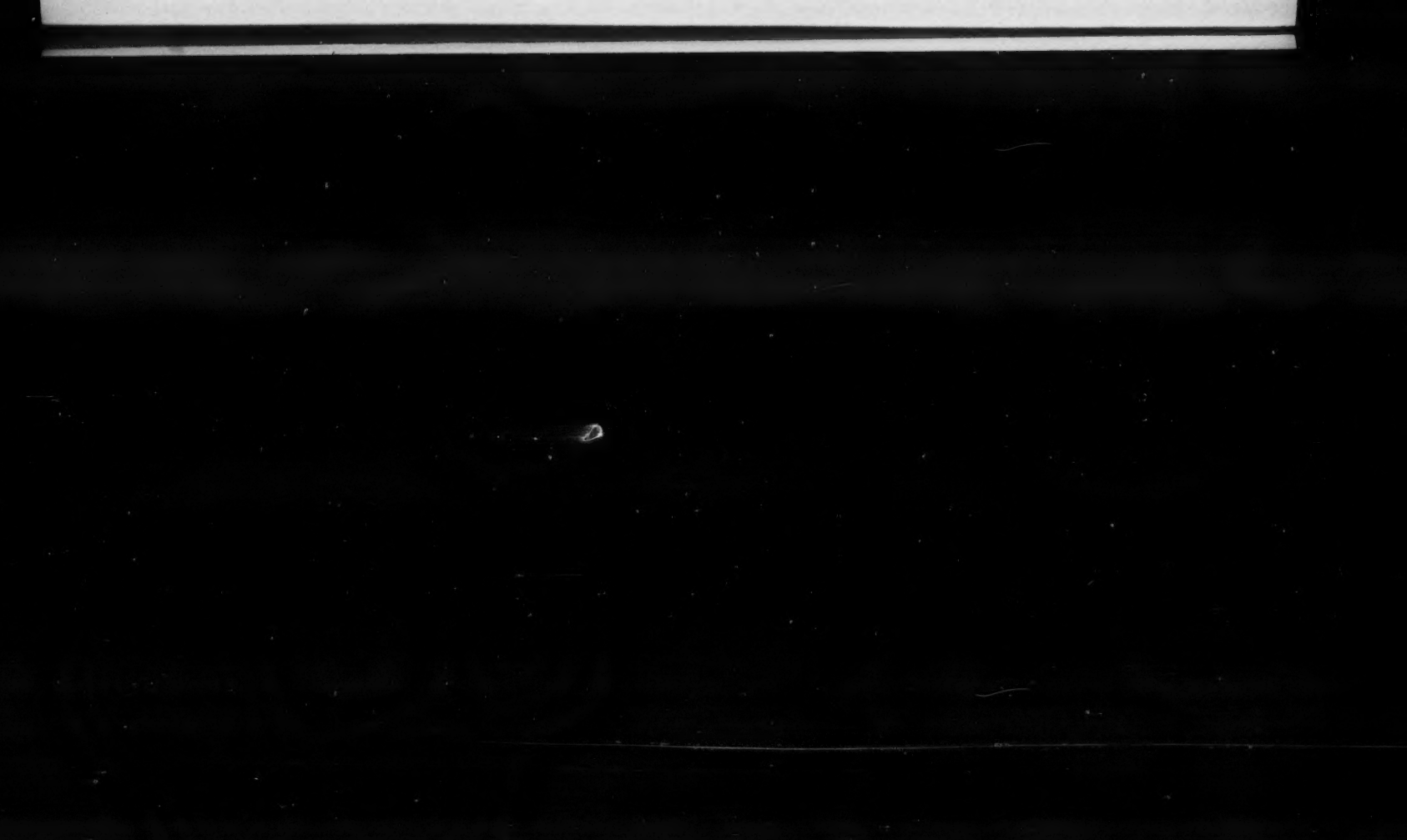
PANSY (13).—The trace-boron pansies were without symptoms of deficiency and, like the violet, this plant proved to be highly sensitive to boron. The edges of the older 5-boron leaves were restricted and had white or burned margins. Marked boron injury was evident even in the youngest leaves of the 10-boron plants, the 15-boron plants were in poor condition and produced few flowers, and all of the 25-boron plants died.

KIDNEY BEAN (14, 15).—Symptoms of diagnostic significance were lacking in trace-boron of both of these plantings. In 1930 (14) only a few green pods were formed by the trace-boron plants, whereas in 1933 (15) the trace-boron plants were relatively fruitful. In 1933 (15) 50 percent of the trace-boron leaves had late-season mildew, only about 5 percent had mildew in 1- and 5-boron, and none in 10-boron. Mild marginal yellowing, burning, and cupping were noted in the 1-boron plants in both years; the injury was severe in 5-boron, and nearly all leaves fell from the 10-boron plants.

COWPEA (16).—Deficiency symptoms were lacking in trace-boron, but the lower leaves developed much mildew just prior to cropping. A few old leaves had mildew in 1-boron, but mildew was absent from 5-, 10-, and 15-boron. The 1-boron plants did not show leaf injury, but the older leaves dropped earlier than in trace-boron. In 5-boron 50 percent of the leaves showed marginal burning; in 10-boron the margins of all leaves were constricted, and all but the youngest showed marginal burning; in 15-boron the plants were severely injured; and the 25-boron plants died (pl. 2, *B*).

JERUSALEM-ARTICHOKE (17).—Deficiency symptoms were lacking in trace-boron. The lower 60 percent of the 1-boron leaves showed

Leaves of various plants, showing symptoms of boron injury. *A*, Lemon. *B*, Persimmon. *C*, Zinnia. *D*, Tomato; this example is highly typical of more advanced injury, which in all respects is like that shown by potato. *E*, Milo; the injury shown by corn is similar. *F*, Alfalfa; not infrequently the chlorotic marginal areas are more sharply defined and have less yellow. *G*, Cotton; in more severe cases yellowing and burned areas are found extending inward from the margins between the larger veins.



A

B

C

some marginal burning with necrotic spots between the veins, but nearly all of these leaves were partly alive when cropped. In 5-boron the leaves on the lower 75 percent of the stalk died, injury was still more severe in 10-boron, and only a few leaves remained alive on the 15-boron plants. Seven seedlings of the deodar cedar (*Cedrus deodara* Laws.) were set in 25-boron in place of the artichoke and made a creditable growth.

LARKSPUR (18).—The trace-boron stalks did not elongate properly, their terminals aborted or died, and the apical portions of many of the leaves became chlorotic or died. The 1-boron plants were normal. Some burning occurred on leaves halfway up the stalks of the 5-boron plants, and bud formation was delayed. These symptoms were progressively more marked in 10-boron, and the flower buds developed poorly. There were few flowers and much leaf abscission on the 15-boron plants, and the 25-boron plants were in poor condition.

ZINNIA (19).—The trace-boron plants were normal. Mild burning occurred along the margins of the 1-boron leaves, and the burning became progressively more severe through each of the successively higher concentrations (pl. 1, *C*).

BARLEY (20).—Boron-deficiency symptoms of morphological character were not in evidence in the trace-boron barley. There were mild symptoms of injury in 5-boron and these became progressively more severe through to 25-boron. In both summer and winter plantings in 1929 the growth of barley in trace-boron was substantially below that in 5-boron, but in both of these plantings mildew was severe on the trace-boron plants. Boron injury in barley is shown by burning of the margins and tips of the leaves. Farther down from the tips, in advance of the mass burning of the tissue, there is some irregular loss of chlorophyll, and small necrotic patches appear between the veins. Barley grown in trace-boron in 1929 was severely attacked by mildew (*Erysiphe graminis* DC.), the amount becoming less as the concentration of boron was increased (*4*); a differential susceptibility to mildew was observed in this planting of 1932, but the attack was not severe even in trace-boron. The spot blotch disease (*Helminthosporium sativum* Pam., King, and Bak.) did not occur in the trace-boron culture but was present in 1-boron and became more severe as the boron concentrations increased. The fact that Christensen (*3*) failed to confirm the writer's observations on the relation between boron concentration and the incidence of disease might represent either differences in barley varieties or in the strains of the organisms; he indicated difficulty in differentiating between boron injury and lesions produced by other causes, but this is hard to understand since boron injury to barley could hardly be confused with spot blotch for the reason that the latter attacks the entire leaf, whereas boron injury is most severe at the leaf tips. Wheat grown in the preliminary experiments in 1929 showed boron reactions similar to those of barley, but mildew was equally severe under all the treatments.

EXPLANATORY LEGEND OF PLATE 2

Leaves of three plants, showing symptoms of boron injury. *A*, Elm; because of its sensitiveness to boron injury and its characteristic markings, the elm is a good boron-indicator plant. *B*, Cowpea; yellowing of young leaves is not always a characteristic of boron injury in this plant or in the similarly sensitive bean; the latter does not always show the pronounced resinous spotting. *C*, Redpepper.

PEA (21, 22).—Symptoms of boron deficiency were lacking in the trace-boron cultures. There was a little leaf injury in 1-boron, and the symptoms became more severe through the remaining cultures.

LIMA BEAN (23).—The tips of the shoots died in trace-boron and some of the leaves showed scattered dead areas. A number of the leaves in 1-boron showed a trace of boron injury, and the marginal burning in 5-boron was marked. The 10-boron plants were badly injured. The 15-boron plants produced no pods, and approximately half of the leaf area was dead when the plants were cropped. There was almost no growth in 25-boron. Three of the five plants in 1-boron were injured mechanically, and the weight (76 gm.) is omitted from table 1.

SWEETPOTATO (24).—The foliage of the trace-boron plants showed no deficiency symptoms, but the tubers were greatly elongated and slender, and none of them would have been marketable. The experiment indicates that tuber shape in the sweetpotato is a function of boron concentration. Tuber diameter, relative to tuber length, increased through the series of treatments, some of the tubers in 25-boron being nearly spherical. The number of marketable tubers in the six cultures was respectively 0, 16, 15, 23, 8, and 3. The greatest weight of roots was in trace-boron. The oldest leaves in 5-boron were burned along the margins, and the injury increased through 10- and 15-boron; in 25-boron all but the youngest leaves showed severe injury.

ONION (25–27).—No deficiency symptoms were observed in the trace-boron plants of either the winter (25) or the summer (26 and 27) plantings. The tips of leaves in 1-boron were burned lightly; the amount of burning increased until, in 25-boron, the leaves were burned back from the tips for 5 to 15 cm. The greatest growth of plants occurred in trace-boron in each of the plantings. It is to be noted that the winter plants accumulated much more boron in their roots, both actually and relatively compared to that in the tops, than did the summer plants.

CARROT (28, 29).—In trace-boron, no deficiency symptoms developed in the plants of either the winter (28) or the summer (29) planting. Injury appeared in a few leaves in the 10-boron plants of the winter planting. In the summer planting a similar amount of injury appeared in the 5-boron plants. The youngest leaves showed mild injury in the 25-boron plants of the winter planting, and marked injury occurred in the corresponding plants of the summer planting.

REDPEPPER (30).—Deficiency symptoms were lacking in trace-boron. The margins of the older leaves in 5-boron were restricted and turned downward. Injury was successively more severe in 10- and 15-boron; and in 25-boron there was a marked reduction in leaf size, accompanied by cupping of entire leaves, with severe marginal burning (pl. 2, *C*).

KENTUCKY BLUEGRASS (31).—Deficiency symptoms were lacking in trace-boron, and the tips of the leaves were green. In 1-boron there was a little mild tip burning that became successively more marked through the series, but this burning was not severe even in 25-boron. The entire plants of the June 1 cropping contained several times as high concentrations of boron as the leaves of the May 4 cropping, indicating a more rapid accumulation of boron during the latter period.

CORN (32, 33).—Morphological symptoms of boron deficiency were not evident in trace-boron. The trace-boron plants (33) matured more slowly than did the plants in the plus-boron cultures. (See milo under 36 and 37 in this connection.) The boron injury of corn resembles that of milo (pl. 1, *E*) and is shown by yellowing between the veins, particularly toward the tips of the leaves, followed and accompanied by marginal and apical burning. Boron injury, first evident in 5-boron, increased to severe in 25-boron.

POTATO (34).—The mesophyll of the trace-boron potato leaves buckled, and the oldest ones were still green when cropped. The oldest leaves in 1-boron showed slight marginal burning, the injury increasing to severe in 25-boron, where more than 50 percent of the leaf tissue was burned and all leaves were cupped. Boron injury in the potato is much like that in the tomato (pl. 1, *D*). The tubers in 25-boron showed some russeting, and these tubers were the only ones entirely free from rhizoctonia. Idaho Russet potatoes planted December 10, 1929, and cropped May 24, 1930, had dry weights in trace-, 5-, 10-, 15-, and 25-boron, respectively, as follows: Tops 21, 31, 37, 35, and 35 gm.; and tubers 88, 117, 172, 82, and 53 gm.

CABBAGE (35).—Deficiency symptoms accompanying the reduction in growth were not in evidence in trace-boron. Some marginal restriction of the leaves in 10-boron was evident. This was more marked in 15-boron, and in 25-boron there was a little mild burning. The marked difference in boron accumulation shown in the covered and exposed leaves is doubtless due to differences both in age and in exposure.

MILO (36, 37).—Morphological symptoms of boron deficiency were lacking in trace-boron, but the trace-boron milo (36) continued to grow and send out new shoots from many nodes after the plus-boron plants had matured. In the second planting (37) the same maturity effect was observed in trade-boron, but because of late planting there was little gain in plant weight. A tendency toward extensive tillering has been noted in boron-deficient cereal cultures by Sommer (*11*), Morris (*10*), and Warington (*13*). The fact that the 25-boron milo plants also exhibited a tendency toward delayed maturity suggests that either a limited supply or a large excess of boron causes milo to behave like sorgo and sugarcane as regards longevity and the translocation of carbohydrates for seed production. Some burning of the leaves developed in 5-boron, the injury increasing to severe in 25-boron (pl. 1, *E*).

CALENDULA (38).—The trace-boron and 1-boron plants were without symptoms. The 5-boron leaves were cupped downward at the margins with a little marginal yellowing. More severe injury resulted in 10- and 15-boron, with severe burning of old leaves and cupping of young ones in 25-boron.

RADISH (39–42).—The trace-boron radishes cropped in February (39) were reduced in size, but splitting was limited to the tips of the fleshy roots; those cropped in November (40) were more angular than those in the plus-boron beds but otherwise were normal; the March (41) radishes were irregularly shaped, the larger ones were split and on standing overnight became spongy, whereas the plus-boron radishes did not; the July (42) trace-boron radishes were reduced in size but otherwise appeared normal. In a winter planting of 1929, the trace-boron radishes weighed only half as much as the 5-boron and there was much splitting. Mild symptoms of boron injury in the form of

marginal burning were shown by the leaves in 10-boron in all plantings, and this injury increased to marked or severe in 25-boron. The extent of boron accumulation both in roots and tops in the higher boron beds corresponds in order of rank with hours of sunshine per day better than with maximum temperature, relative humidity, or evaporation.

OATS (43).—Deficiency symptoms were lacking in trace-boron. The planting was cropped when it had just started to ripen, because of rank growth and lodging. The boron injury was mild in 5-boron, increasing to severe in 25-boron.

CELERY (44).—The hearts of all the trace-boron plants were badly rotted, and the petioles were discolored and transversely cracked on the lower surface; only the older leaves were alive when the plants were cropped. The leaves of the 25-boron plants were reduced in size and thickened, but there was no burning. The 1-, 5-, 10-, and 15-boron plants were essentially equal in appearance, and all had flower stalks upward to 60 cm. tall.

MUSTARD (45).—Deficiency symptoms were not observed in trace-boron. Mild boron injury, represented by marginal yellowing of the leaves, was shown in 5-boron; the injury increased to 25-boron, where 60 percent of the leaves had restricted, yellowed, and burned margins.

PARSLEY (46).—The trace-, 1-, 5-, and 10-boron plants were essentially alike and showed no deficit or injury symptoms; all were vigorous, bushy, compact plants about 40 cm. tall. The 15-boron plants were uniformly reduced in size (30 cm. tall) but showed no leaf injury. The 25-boron plants were without leaf markings and all remained alive, but they were very small.

ALFALFA (47–49).—The characteristic yellowing of boron-deficient alfalfa was not noted in these plantings, but in a summer planting in 1929 the terminal growth was notably yellowed and the trace-boron growth was poor. In the July cutting of 1931 (48), there was little or no growth depression in trace-boron and the stand was maintained, but by the final cropping in September only 16 of the original 20 plants were alive. Loss of stand also occurred in higher boron concentrations both in this planting and in the preceding winter planting (47). In 15- and 25-boron the margins and tips of older leaves yellowed and occasionally burned (pl. 1, *F*).

LETTUCE (50, 51).—There were no deficiency symptoms in either of the varieties of lettuce in these summer plantings, and flowering was not delayed. In an earlier winter planting that rotted out during a period of rainy weather, the growth in trace-boron was very poor and only fair in 1-boron, whereas good heads were forming in 5-boron. These summer plantings (50, 51) developed mild marginal burning in 1-boron, the injury increasing to 25-boron. In the latter concentration the margins of all leaves were burned, the older ones severely so.

TOBACCO (52).—No deficiency symptoms were apparent in the trace-boron plants. Marginal burning with interveinal yellowing occurred in 10-boron, and in 25-boron the leaves were cupped, with marginal burning and dead spots between the veins. Intermediate injury developed in 15-boron.

VETCH (53).—Deficiency symptoms were lacking in trace-boron. The oldest leaves showed a little boron injury in 5-boron; injury increased through 10- and 15-boron; and in 25-boron even the youngest

leaves burned. No nodules developed on the roots in trace-boron; they were few in 1-boron, abundant in 5-boron, reasonably so in 10-boron, few in 15-boron, and none in 25-boron.

TOMATO (54, 55).—There was no evidence of deficiency symptoms in the trace-boron plants of either of these plantings. Mild boron injury was evident in 5-boron, and the injury increased to 25-boron, where the leaves were reduced in size, cupped, and burned (pl. 1, *D*).

CALIFORNIA-POPPY (56).—Boron-deficiency symptoms were lacking in trace-boron. The 1-boron plants were likewise normal. A few 5-boron leaves showed mild injury, and the injury increased to 25-boron, where it was substantial. The burned tissue turned black, a reaction not observed among the other plants tested.

TURNIP (57).—Boron-deficiency symptoms were lacking or uncertain in trace-boron. There was only mild leaf injury in 25-boron. The plants in 10-boron made a poor start and were irregular when cropped.

COMMON BEET (58, 59).—Deficiency symptoms in the winter-grown beets (58) were limited to a shallow crack in one root. The summer beets showed marked deficiency; the leaves were small, one root had heart rot, and two had advanced dry rot. Only obscure injury was observed in the leaves of the winter 15-boron plants (58), and the injury was mild in 25-boron. Leaf injury was evident in the 10-boron plants of the summer planting (59), increasing to pronounced in 25-boron.

LEAF BEET, OR CHARD (60).—Though without morphological symptoms of boron deficiency, the trace-boron chard wilted repeatedly during the middle of the warmer days, but no wilting was observed in the plus-boron plants. Beets in trace-boron occasionally reacted similarly, but the wilting was never so pronounced as in the chard. In contrast to this observation in chard and beets, Warington (*13*) has reported that the broadbean (*Vicia faba* L.) remained turgid in minus-boron cultures at times when plus-boron plants wilted. The older chard leaves in 25-boron were restricted at the margins and showed mild burning.

MUSKMELON (61).—Mildew was severe in trace-boron, decreasing to very little in 10-boron, with none in 15- or 25-boron. There were many dead and partly dead leaves in trace-boron but fewer in 1-boron; this difference may have been due to the difference in mildew. A few 5-boron leaves showed a little boron injury, and the injury increased to 25-boron, where all leaves were cupped and the older ones badly burned.

SWEETCLOVER (62, 63).—Deficiency symptoms were absent from trace-boron. Injury was first apparent in the 10-boron plants of both the winter and the summer plantings, but in neither planting did it become severe in 15- and 25-boron.

SWEET PEA (64).—Occasional dead areas developed in the trace-boron leaves, but the plants were otherwise normal. Mild injury symptoms occurred in 5-boron, and the injury though marked was not severe even in 25-boron.

SUGAR BEET (65–68).—Boron-deficiency symptoms of varied severity developed in the trace-boron cultures in the summer plantings of 1930, 1931, and 1933 (66–68), but the beets grown during the winter of 1930–31 (65) were normal. Boron deficiency in beets, as is now well known, results in a dry rot of the roots and a heart rot at the crown of the plant, and in addition it sometimes kills the young leaves or prevents their growth. It may result, as in crop 66 (fig. 2),

in the death of the older leaves, where deterioration typically starts at the margins and progresses inward. The mesophyll of the leaves of affected plants is notably buckled. The foregoing disorders of the beet were first ascribed to boron deficiency by Brandenburg (*1*) in 1931. Injury due to excessive boron was shown in 25-boron by restriction and burning of the leaf margins, but in no instance was the injury severe.

OXALIS (69).—Many leaves in trace-boron were semichlorotic and exhibited marginal abnormalities, necrotic spots appearing in the

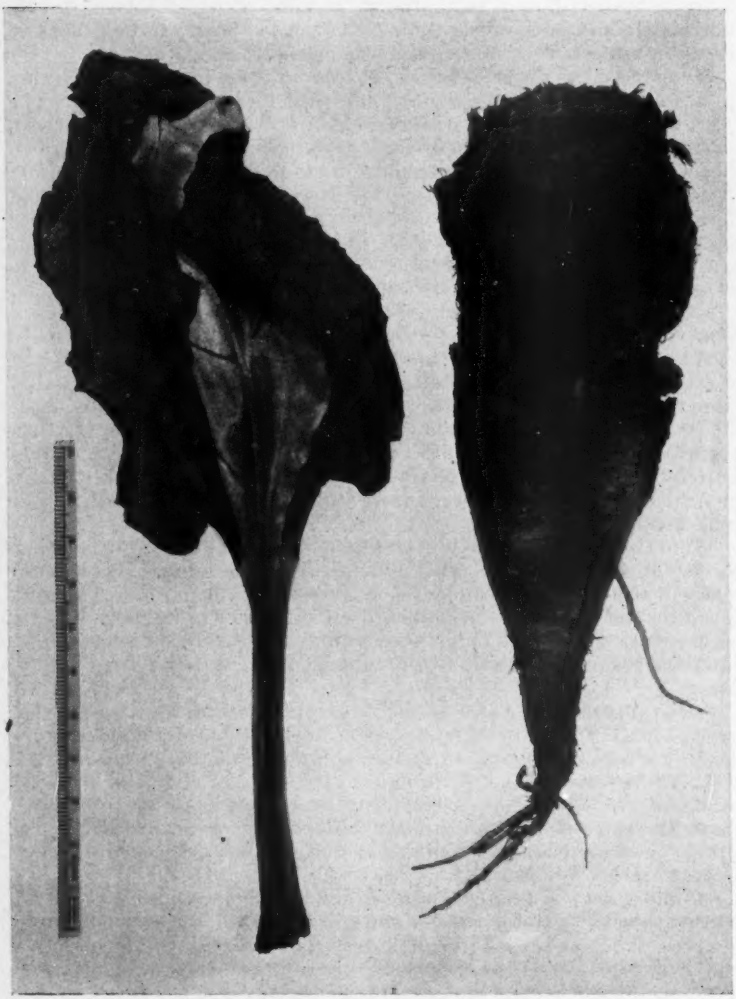


FIGURE 2.—Boron-deficiency symptoms in sugar beet; this example is taken from the plants reported under crop 66.

mesophyll. There were no morphological symptoms of boron injury in any culture.

COTTON (70).—The trace-boron cotton leaves both in this planting and in a 1929 planting were characterized by chlorotic blotches, large irregular dead areas, and buckled mesophyll. The plants had a compact appearance due to reduced branch lengths, and few or no bolls were set until October. Mild marginal burning of the leaves occurred in 10-boron, and the injury to leaves increased to severe in 25-boron (pl. 1, *G*). The numerical formula here employed for measuring relative tolerance is not very well suited to plants such as cotton that make substantially more growth with 5 or 10 p. p. m. of boron than in trace or 1 p. p. m. but which are substantially injured in 15 or 25 p. p. m. As previously noted, the reactions of a 1929 planting of cotton paralleled this test, but in a 1931 planting that had to be cropped in September before any bolls had matured, the trace-boron plants started to set bolls in late August. The boron content of these trace-boron plants was not out of line with that of the other two plantings.

ARTICHOKE (71).—The trace-boron plants were chlorotic, the petioles broke easily and clean, the floral stalks did not elongate normally, and the floral buds were about 2 cm. in diameter. The color of the 1-boron plants was excellent, the main floral buds were 6 cm. in diameter, and the flower stalks were 30 and 50 cm. tall; each plant had 3 secondary buds. The 5-boron plants were larger than the 1-boron, the main buds were 8 cm. in diameter, and the flower stalks were each 60 cm. tall. Mild boron injury appeared in the older leaves. The 10-boron plants produced buds 3 and 5 cm. in diameter on 40-cm. stalks; boron injury was marked but confined to the older leaves. The bud development in 15-boron was similar to that in 10-boron, and some injury was evident on half of the leaves. The 25-boron plants and their floral buds were further reduced in size, and as much as 60 percent of the leaf tissue of the older leaves was burned. The data indicate that this plant might respond to boron under field conditions. The fact that artichokes do remarkably well in the Half Moon Bay area of the central California coast supports the evidence drawn from other crops that boron requirements are lower under conditions of reduced light intensity. In this coastal area the skies are overcast much of the time.

ASPARAGUS (72).—The plants growing in trace-boron were small; there were many dead stems, and one plant died. There was some boron injury in the tips of plants growing in 25-boron. Only one of the five plants in 10-boron made a satisfactory start, and those results are accordingly omitted from table 1. The approximate average height of plants in the six cultures was respectively 40, 60, 80, 65, 100, and 80 cm. Asparagus plants remained alive for 3 years in a culture supplied with solution containing 100 p. p. m. of boron.

DISCUSSION

The data on the reactions of the 50 botanical species and varieties of plants to boron, presented in table 1 and in the notes on plant symptoms, provide a substantial basis for the conclusion that there is some overlapping of the beneficial and injurious effects of boron within plants. At least mild leaf injury was observed in 19 of the

72 plantings at or below the boron concentrations that resulted in greatest growth. This finding is entirely compatible with the view that boron is carried into the leaf in the transpiration stream and that from the leaves there is little re-movement of boron with the sugars and other compounds passing out of the leaves to the fruit and other tissues (stone fruits are known to be an exception). So much boron may accumulate in the older leaves of a plant that yellowing or burning results, while at the same time the boron supply to actively enlarging meristematic tissues is insufficient for their most rapid growth.

Because of the indications of an overlapping between the beneficial and injurious effects of boron within a plant, any conception of an optimal concentration in the substrate becomes theoretical and is certainly relative to other conditions. It is a matter of convenience, notwithstanding, to review the data presented in table 1 under the conventional headings Boron Deficiency and Boron Toxicity.

Of the 72 croppings, including the repetition of varieties grown in more than one season, the best growth occurred in the respective beds the following number of times:

Boron concentration (p. p. m.):	*Distribution of best growth*
Trace	19
1	20
5	20
10	7
15	6
25	—

Thus over 70 percent of the plantings responded to more than a trace (0.03 to 0.04 p. p. m.) of boron, and about 45 percent of the varieties made better growth with 5 p. p. m. or more of boron than with less than that amount.

BORON DEFICIENCY

Of the 58 varieties of plants, 20 developed morphological symptoms of deficiency; the maturity of 4 was prominently affected; and 4 were more subject to mildew (*3, 4, 16*) in the trace-boron culture than in the higher concentrations.

Boron deficiency in barley was shown by a notable susceptibility to mildew; in corn, by delayed maturity; in milo, by continued vegetative growth after maturity had occurred in the intermediate boron treatments; in alfalfa, by loss of stand and reduced growth with or without yellowing of upper leaves; in artichokes, by chlorotic, undersized plants, brittle petioles, and repressed floral development; in asparagus, by reduced growth and death of stems; in lima beans, by death of plant tips and dead areas in leaves; in kidney beans, in one crop, by poor development of pods and root nodules and susceptibility to mildew; in cowpeas, by mildew; in beets, by deterioration of old leaves, dry rot, heart rot, and death of some plants; in celery, by rotting of hearts and by transverse cracking and discoloration of petioles; in leaf beets, by daily wilting; in cotton, by chlorotic blotches, buckling, and dead areas in the mesophyll, and by extensive abscission of floral buds or by delayed fruiting; in muskmelons, by excessive mildew; in potatoes, by buckling of mesophyll; in radishes, by irregularly shaped and spongy storage roots with splitting of the larger ones; in sweetpotatoes, by slender and greatly elongated tubers; in sweet

peas, by necrotic spotting of leaves; in blackberry, by buckled mesophyll and loss of dominance of the terminal buds; in cherry, by chlorotic midsummer leaves with tips of serrations resinous or dead; in the elm, by yellowing of leaves late in the season with dead areas along the margins; in the fig, by shortened internodes, chlorotic and misshapen leaves with dead areas, and loss of dominance of the terminal bud; in grapes, by buckled mesophyll and irregular dead areas along the leaf margins; in the persimmon, by dead or chlorotic leaf margins; and in the date palm (not included in table 1), by lack of stiffness and finer growth of fronds.

The extent to which symptoms were developed and growth was curtailed by boron deficiency was often at variance when the same variety was replanted, not only as between winter and summer plantings, but also as between successive summer or winter plantings. Sugar beets (table 1, crops 65 to 68), as grown during each of three summers, were markedly deficient in the trace-boron culture, but in a winter planting there was no evidence of deficiency. Similarly, common beets (crops 58 and 59) were deficient in a summer trace-boron planting and normal in a winter planting. Radishes (crops 39 to 42), on the other hand, were normal other than for size in a summer planting, angular in a fall planting, and showed deficiency symptoms of the fleshy roots in each of two winter plantings. Alfalfa (crops 47 to 49) developed no marked deficiency in either the winter or summer planting in 1931 but was markedly deficient in the summer of 1929. Onions were normal in the trace-boron culture irrespective of time of planting or harvest.

The lack of uniformity in the response of a number of the plants to trace-boron resulted in a reluctance on the part of the writer to publish the data without some explanation. In attempting to account for the apparent discrepancies, consideration was first given to the possibility that some other element, introduced with the nutrient salts as an impurity, replaced boron. Greenhouse investigations, in which cotton was the principal test plant, involved trials with a series of elements, including many of those tested by Brenchley and Warington (*2*) and, in addition, gallium, scandium, germanium, and indium. With the possible exception of scandium, the results were negative. Scandium sometimes seemed to give a slight response, and it has since been learned that the salt employed was high in magnesium and contained only a little scandium. Spectroscopic examination of the culture-solution salts and plant material likewise failed to provide evidence that other elements were involved as a cause for the differences.

An explanation for the seasonal differences in boron requirements was also sought in another direction. As reported elsewhere (*6*) the growth of cotton seedlings in minus-boron solutions was found to be improved and the severity of certain of the boron-deficiency symptoms reduced when small amounts of indole-3-acetic acid were added daily to the nutrient solution. The advantageous effects of the indole-3-acetic acid were most marked when the plants were grown under reduced light. Although these results might be interpreted as indicating that boron is essential to the formation of auxin in plants, an alternate suggestion is that the indole-3-acetic acid increased the movement of the traces of boron from the cotyledons to the meristematic tissues.

Evidence that photoperiod reactions are not primarily involved is supplied by the work of Warington (*13, p. 455*), who reached the following conclusion:

> Within the range of 7–16 hours, the length of day has no bearing on the need of the plant for boron, since with one possible exception, where the case remained unproven * * * the deficiency symptoms characteristic of a lack of boron were similar under both long and short day conditions, although they were less pronounced and their rate of progress retarded if the days were short.

In Warington's work the day length was shortened by placing plants in dark chambers overnight with temperatures and midday light intensities unchanged. That work accordingly does not provide an opportunity for specific deductions on relations between high light intensities and the boron requirements of plants; the differences found by Warington in the time of appearance of symptoms are, nevertheless, in the direction to be expected on the basis of the light-auxin relationships cited above. This subject will receive further consideration in the section dealing with the movement of boron in plants.

A direct analysis of the data of table 1 for relations between boron deficiencies and average light intensities is not possible, as the average number of hours of sunshine per day does not constitute a satisfactory index to light intensity, particularly when different summers or different winters are compared in a region where thinly overcast skies (high fogs) occur frequently but irregularly during the morning hours.

BORON TOXICITY

In table 1 the plantings are arranged in an order related to their relative tolerance to boron. To determine this order, tolerance was estimated by dividing the average of the plant weights in 5-, 10-, and 15-boron by the weight in trace- or 1-boron, whichever of the two was the higher; the quotient ($\times 100$) is recorded as relative tolerance. The first nine plants of the series did not survive in boron concentrations as high as 15 p. p. m., and for this reason their tolerances are not indicated numerically. These plants are given a position in the table on the basis of relative growth in trace-, 1-, and 5-boron. The foregoing procedure is quite arbitrary, and neither the positions of the plants in the table nor the numerical values can be regarded as highly definite. The prevailing climatic conditions during growth had marked effects on the reactions of the plants to boron, and the same plant reactions did not result when a plant was grown during each of several seasons. The position of a plant such as cotton, for example, which grew best in a number of seasons in 10-boron, is too far along in the series if its behavior in 15- and 25-boron is compared with that of beets or asparagus.

The series of plants have been broadly classified into three groups by designating those whose relative-tolerance values were below 50 as *boron-sensitive plants*, those whose relative-tolerance values were between 50 and 100 as *boron-semitolerant plants*, and those whose relative tolerance values were above 100 as *boron-tolerant plants*.

The notable differences in the boron-tolerance values of different plants of the series are shown graphically in figure 3. In general, the growth depressions that resulted with increasing concentrations of boron in the substrate tend to be linear. The plants illustrated in

figure 3 were chosen to show the marked differences in the slopes of the growth-depression curves.

BORON ACCUMULATION

Effect of Boron Concentration in Nutrient Solution

The data presented in table 1 show outstanding differences in the boron-accumulation characteristics of the different species compared. The concentrations in the leaves of plants growing on the 5-boron solution ranged from 58 to 1,804 p. p. m. and in 25-boron from 209 to 3,875 p. p. m. The roots, stems, and fruits customarily contained

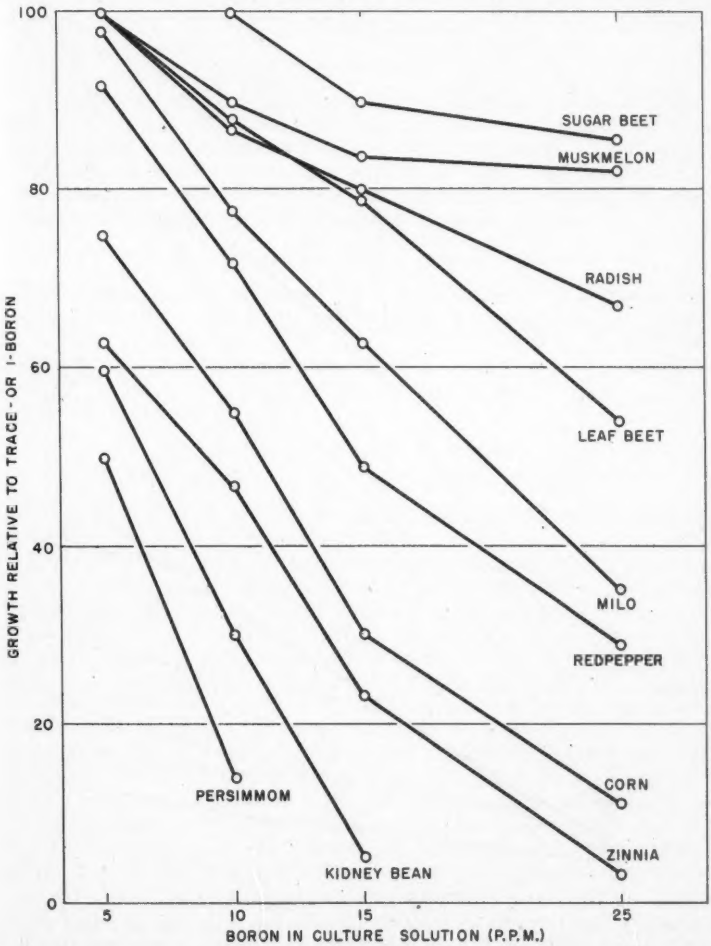


Figure 3.—Effect of boron on growth of plants, showing tendency toward linear relations between boron toxicity and the boron content of the substrate.

only a little boron as compared with that found in the leaves, but to this generalization peach and cherry are important exceptions.

The boron concentrations in the leaves of plants on trace-boron amounted (on dry-weight basis) to 100 to 5,000 times the concentration of boron in the nutrient solution; ratios between 400 and 1,200 predominated. On the 1-boron culture the accumulation ratios, on the same basis, ranged from 22 to 519, values between 50 and 200 predominating. In nearly all instances the accumulation ratios were substantially lower on 5- to 25-boron than on 1-boron, and many

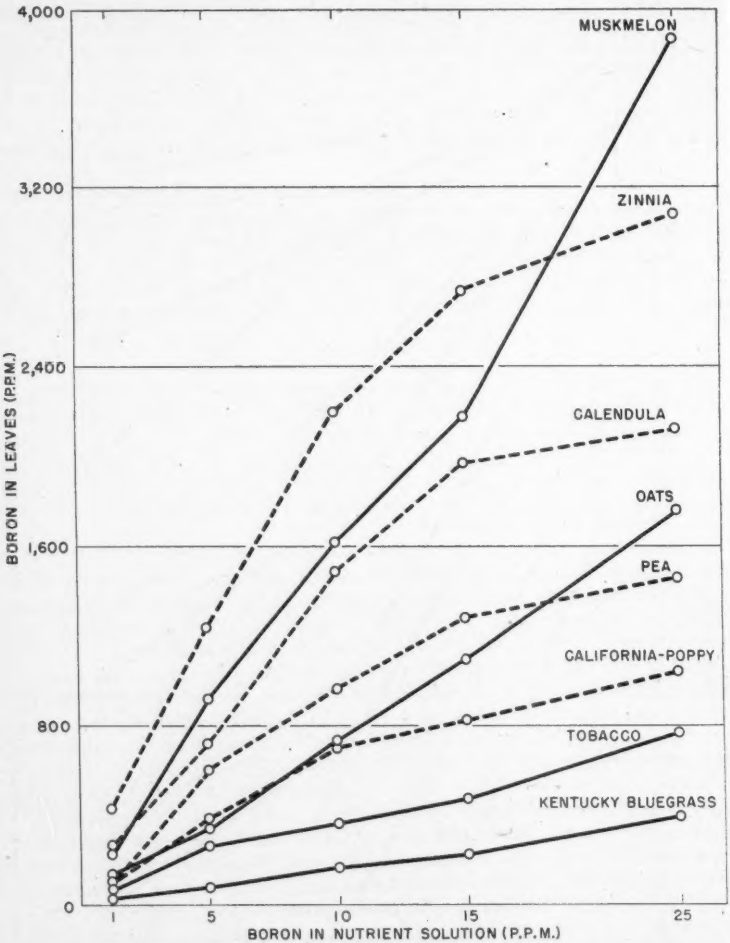


FIGURE 4.—Accumulation of boron in leaves of plants on solutions with 1 to 25 p. p. m. of boron. Solid lines=plants with linear accumulation ratios; broken lines=plants with decreasing ratios.

plants showed little change in their accumulation ratios between 5 and 25 p. p. m.

Between 5- and 25-boron, the series of plants tend to fall into one or the other of two groups: (1) Those with accumulation ratios that changed little (fig. 4) as the solution concentrations increased (accumulation linear) and (2) those that had well-defined decreasing ratios with the successively higher solution concentrations. Of the full series of plants, about as many tend to fall into one group as the other, but there are also a good many plants whose accumulation characteristics in the 5- to 25-boron range are not well defined by the data. The position of plants in one or the other group bears little relation either to the position of the plants as listed in order of tolerance or to position in terms of boron accumulation from the 5-boron solution.

Effect of Climatic Conditions

A general one-way relationship between climatic conditions and the extent of boron accumulation apparently does not exist. Of those plants included in both summer and winter planting, the onion and alfalfa accumulated more boron during the short-day cooler months than during the summer, whereas the opposite relationship was found in carrots, bluegrass, radishes, beets, and sweetclover.

Tolerance and Boron Accumulation

The correlation, as indicated by the data, between boron toxicity and the extent to which different species accumulate boron from a given substrate is apparently quite low. This fact is illustrated graphically by the scatter diagram (fig. 5), wherein boron concentrations in the leaves or laminae of the 5-boron plants are plotted against the relative-tolerance values.

MOVEMENT OF BORON IN PLANTS

Distribution of Boron in Different Parts of Plants

With the stone fruits as known exceptions (*8*), boron tends to accumulate in highest concentrations in the leaves of plants and to be present in relatively low concentrations in roots, wood, fruit, and other storage and meristematic tissues. In other words, having been carried into the leaves, presumably in the transpiration stream, it seems that there is a comparatively limited re-movement of boron. An examination of the distribution of boron in lemon leaves makes it evident, furthermore, that boron moves from the veins into the interveinal leaf tissues and toward the leaf margins and that there is comparatively little back movement through the mesophyll. The combined midveins and petioles, the green, the yellow, and the dead marginal portions of lemon leaves were found in one examination to contain respectively 47, 438, 1,060, and 1,722 p. p. m. of boron on the dry-weight basis, a distribution of boron that corresponds with the pattern of injury (pl. 1, *A*). A similar distribution has been found in walnut leaves (*8*), and the pattern of injury in many other plants suggests that this situation may be fairly general. Boron, on the other hand, is quite freely translocated from one region to another in the stone fruits, and it is probable that intermediate degrees of boron movement take place in other plants.

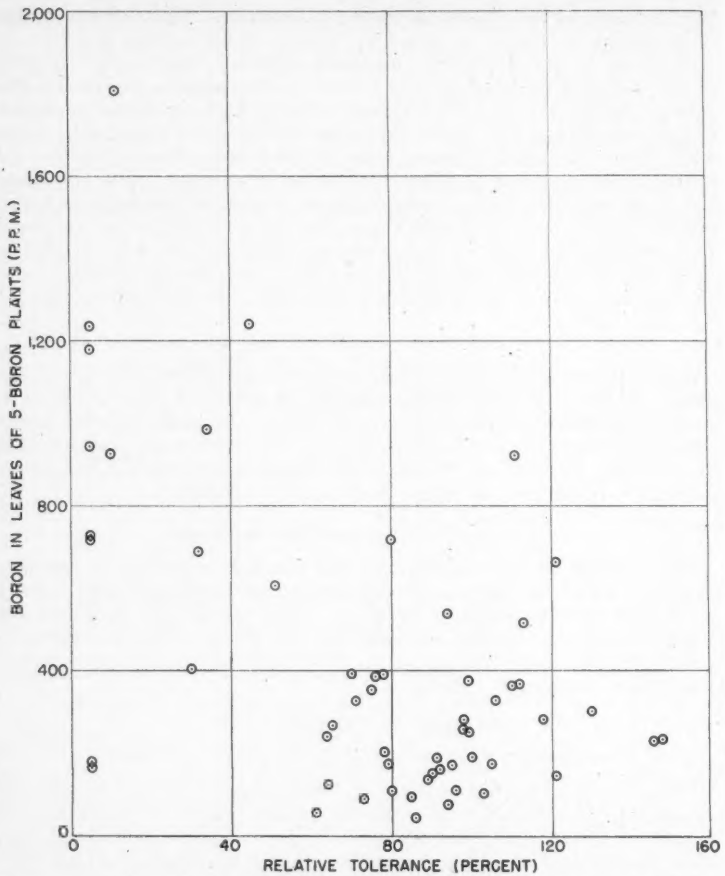


FIGURE 5.—Accumulation of boron in leaves of plants grown in 5-boron solution and the relative tolerance of these plants.

SOLUBILITY OF BORON IN LEAF TISSUES

The evidence of only a limited re-movement of boron from the leaves of many plants presents a question as to whether, after entering the mesophyll from the transpiration stream, boron is precipitated in the form of compounds of low solubility or whether it is combined in soluble molecules of such size or character that they are unable to re-pass the plasma membranes for movement to the other parts of the plant. The measurements presented in table 2 were made for the purpose of examining this question by comparing the concentrations of boron found by analysis in the expressed saps of a series of plants with the concentrations of boron calculated as possible in the same saps on the basis of the sap content of fresh leaves and analyses of the dried leaves.

If much or all of the total boron known to be present in leaves was found in the press cake, one would conclude that it had probably existed in the leaf in an insoluble form. If, on the other hand, the boron concentrations found in the sap expressed from leaves accounted for all or nearly all of the total boron, then it would be logical to conclude that much of it had been present in the sap in the form of soluble but immobile molecules.

TABLE 2.—*Concentrations of boron in expressed leaf sap and the concentrations indicated as possible on the basis of analyses of the dry leaves*

PLANTS WITH LITTLE OR NO PRECIPITATED BORON

Plant, date cropped, and boron concentration (p. p. m.) of nutrient solution	Boron in—		
	Dry leaves (by analysis)	Leaf sap	
		Calculated as possible	Found by analysis
	P. p. m.	*P. p. m.*	*P. p. m.*
Alfalfa (May 4, 1933):			
Trace	30	4	[1]
1	199	32	31
5	272	46	38
10	343	60	54
15	531	94	115
25	822	147	176
Sugar beet (crop 68):			
Trace	19	2	2
1	106	9	7
5	234	21	20
10	495	44	46
15	588	51	51
25	975	83	95
Calendula (Aug. 14, 1933):			
Trace	54	3	4
1	231	13	
5	604	38	34
10	1,226	79	91
15	1,726	114	111
25	2,298	189	184
Cowpea (crop 16):			
Trace	32	3	[1]
1	119	13	6
5	404	45	50
10	722	78	86
15	1,132		
25			
Kentucky bluegrass (crop 31, May):			
Trace	3	1	[1]
1	22	6	2
5	92	27	17
10	164	40	42
15	224	65	61
25	398		
Lettuce, Los Angeles Market (crop 50):			
Trace	27	1	[1]
1	70	2	[1]
5	116	4	2
10	221	7	8
15	343	13	12
25	582	25	29
Lettuce, Big Boston (crop 51):			
Trace	43	2	3
1	75	2	2
5	166	7	7
10	353	14	12
15	459	23	24
25	817	46	46
Kidney bean (crop 15):			
Trace	[1]	[1]	3
1	151	20	20
5	690	91	83
10	1,254	201	190
15	1,733		
25			

[1] Trace.

TABLE 2.—*Concentrations of boron in expressed leaf sap and the concentrations indicated as possible on the basis of analyses of the dry leaves*—Continued

PLANTS WITH LITTLE OR NO PRECIPITATED BORON—Continued

Plant, date cropped, and boron concentration (p. p. m.) of nutrient solution	Boron in—		
	Dry leaves (by analysis)	Leaf sap	
		Calculated as possible	Found by analysis
	P. p. m.	*P. p. m.*	*P. p. m.*
Pea (crop 21):			
Trace	6	2	(1)
1	212	33	31
5	609	118	116
10			
15	1,283		
25	1,452		
Tobacco (crop 52):			
Trace	19	2	1
1	72	5	5
5	261	20	16
10	365	26	28
15	474	35	45
25	771	54	56
Turnip (May 3, 1933):			
Trace	22	2	(1)
1	84	6	3
5	189	13	9
10	258	22	14
15	446	34	31
25	744	64	68
PLANTS WITH MUCH PRECIPITATED BORON			
Muskmelon (crop 61):[2]			
Trace	30	3	1
1	234	20	13
5	1,010	92	37
10	1,835	151	78
15	2,249	204	109
25	3,836	323	191
Sweetpotato (Aug. 15, 1933):			
Trace	57	5	(1)
1	152		
5	706	88	49
10	1,301	138	108
15	1,646		
25	2,506		
Tomato (crop 55):			
Trace	34	3	1
1	103	9	4
5	253	23	19
10	531	51	26
15	684	61	34
25	1,168	133	82

[1] Trace.

[2] Boron in green leaves (dry basis). The weighted means of green and dead leaves were reported in table 1.

Aliquots of freshly picked leaves, packed in well-stoppered, long, glass test tubes, were frozen in solid carbon dioxide overnight; the material was then quickly thawed and the sap expressed as rapidly as possible in a Carver press at 2,400 pounds' pressure per square inch. The "possible" concentration of boron in the leaf sap was computed by dividing the oven-dry weight of the press cake by the weight of sap (difference in weight of the fresh sample and oven-dry press cake) and multiplying the quotient by the parts per million of boron found in a dried aliquot of the original leaf material. Some uncertainty must accompany estimates of this character both as regards changes in solubility during freezing and pressing and as regards the proportion of the leaf water that functions as a solute in living tissue. It seems

doubtful, nevertheless, that the issue here under examination could be wholly confused by these considerations.

The data of table 2 indicate the existence of 2 classes of plants: (1) Those having little or no insoluble boron in their leaves, and (2) those having substantial quantities of insoluble or slightly soluble boron. Of the 14 kinds, 11 fell in the former class and 3 in the latter. In each of the latter 3 kinds (muskmelon, sweetpotato, and tomato) 50 percent of the boron is indicated as having been insoluble or fixed. Notwithstanding this evidence of some insolubility in the latter 3 kinds, the concentrations of soluble boron in all the expressed leaf saps were so high that the low concentrations in the stem and root tissues cannot be explained on the basis of insolubility. Any theory advanced to account for the immobility of the boron in leaves that assumes precipitation with organic or inorganic constituents of the leaf cells would require, if valid, that essentially all of the boron in the leaves should be insoluble. In none of these plants was that found to be the case, yet in all of them the boron concentrations in tissues other than the leaves were by comparison relatively low (table 1). It is most logical to conclude, therefore, that the low mobility of boron after having entered the leaf mesophyll is due not to insolubility but instead to some inability of the soluble molecule of which the boron evidently becomes a part to move out of the cells.

It is well known that boron unites freely with a number of sugar-like substances. The fact that before reaching the leaf mesophyll boron, like other inorganic constituents, must pass through living cells of the root implies that the reaction taking place in leaves may be either photochemical or one that takes place with photosynthetic products occurring in higher concentrations in leaves than elsewhere. Other observations (table 1) likewise indicate that light is in some manner a factor that limits boron movement.

The concentration of boron in the roots of onions, radishes, and carrots was higher, relative to that in the leaves, when these plants were grown as winter crops than as summer crops. The bulbs of onions cropped from the 25-boron bed in April (table 1, crop 25) contained three times as high a concentration of boron as those cropped in July (crop 26), and yet the concentrations of boron in the leaves of the two crops were similar. The roots of 25-boron radishes (crops 39 to 42) cropped in February, November, March, and July had concentrations respectively 47, 31, 24, and 16 percent as high as the leaves, and the corresponding average daily hours of sunshine were 6.4, 7.8, 8.0, and 12.1. Carrots cropped from the 25-boron bed in April (crop 28) and September (crop 29) had respectively 788 and 1,244 p. p. m. of boron in their leaves and 319 and 114 p. p. m. in their roots; the average hours of sunshine per day for the carrots were 9.5 and 11.0 respectively. In all of these plants retention of boron in leaves increased as hours of sunshine increased. Beets did not accumulate much boron in their roots in any planting, and the differences between summer and winter plantings are of doubtful significance.

As shown by the foregoing and the example provided by the stone fruits, there is evidently a wide difference between plants in the extent of boron movement from leaves to other parts. Attention has been called previously (7) to a 40 percent greater accumulation of boron in leaves of sunflower on basal branches of plants with grafted-in

Jerusalem-artichoke tops than in similarly situated sunflower leaves on plants without Jerusalem-artichoke tops. This finding was thought to mean that less boron was fixed in Jerusalem-artichoke than in sunflower leaves and that a movement occurred from the former to the latter.

Boron Movement and Boron Deficiency

Little has been said in this paper about relations between the severity of boron-deficiency manifestations and the concentrations of boron found by analysis in the leaves of the plants. The omission is occasioned in part by the possibility that many of the variations shown in the boron analyses of the trace-boron plants are within the range of the analytical error for plant material. On the other hand, good correlations might not have been found in this borderline, or marginal, range even if the leaf analyses had all been highly accurate. The marked differences between plants in the ratios of boron in leaves to boron in other parts, the differences in accumulation in roots between winter and summer plantings, and the variations in the severity of deficiency symptoms in winter and in summer all point to the importance of the boron-movement factor. The importance of this factor is further illustrated by the observation of a number of investigators that deficiency symptoms appear quite soon after plants are transferred from plus- to minus-boron solutions. The observation undoubtedly means that little of the boron present in the older leaves is moved into the developing meristematic tissues. In other words, the boron concentration found in leaf tissues does not necessarily provide a criterion of the concentrations present in the actively growing tissues of the plant and for normal growth the boron evidently must be present in the tissue concerned. Within the marginal ranges of soil boron concentrations, factors influencing the movement of boron into meristematic tissues from leaves may thus be almost as important in terms of boron deficiency as the boron-supplying power of the soil itself.

There is no evident reason for believing that the movement of boron into terminal buds or other growth tissues that utilize materials translocated from leaves is conditioned by factors very different from those determining the movement of boron from leaves to the roots. The data relating to such translocation may appropriately be examined for parallelisms between climatic factors and the accumulation of boron in root tissues and between climatic factors and boron deficiency.

Plants grown both in summer and winter had less boron in their roots, relative to that in their leaves, in summer crops than in winter crops, and the summer crops tended to show the most marked manifestations of boron deficiency. More marked symptoms of deficiency developed during the relatively bright summer of 1929 than during subsequent summers. Radishes, like other plants, had more boron in their roots, relative to the concentrations in the leaves, in winter than in summer; yet, in contrast with other plants, the deficiency symptoms were most marked in the winter. This apparent discrepancy in the relation between high light intensity, restricted boron movement, and deficiency symptoms is clarified when attention is directed to the fact that the symptoms of boron deficiency exhibited

by the radish were confined to the root tissues and in actual concentration there was less boron in the radish roots in the winter than in summer.

There is a widely prevalent and apparently well supported idea that boron deficiency is more pronounced in dry summers than in rainy ones. Inasmuch as dry summers are usually characterized by a predominance of bright days, the possibility exists that the apparent relationship between moisture conditions and boron deficiency is more truly a relationship between average light intensity and boron deficiency. The data presented in this paper are not sufficient to warrant the definite conclusion that light intensity is a dominant factor determining the extent of boron deficiency when plants are grown with a marginal supply of boron during dry seasons, but the limited evidence points in that direction. Long before boron deficiency was recognized as a cause of the drought spot and related diseases of apples, Mix (*9*) concluded that these diseases were "greatly influenced if not caused by lack of sufficient moisture, but insufficient moisture cannot be looked upon as the sole cause." A similar conclusion has been reached by a number of subsequent investigators of these disorders of the apple. Walker and his associates (*12*) have likewise reported that boron deficiency in beets is most pronounced in dry summers.

Drying has been found to be an important adjunct to boron fixation when new boron is added to a soil, but there is as yet no evidence that drying reduces the boron concentration of the soil solution when new boron is not added. On the contrary the concentration of boron in the soil solution has been found to be higher at the moisture equivalent than at higher moisture percentages. When soils without added boron were dried and then rewetted the initial boron concentrations were again found.

SUMMARY

For the purpose of obtaining comparative data on symptoms, growth reactions, and boron-accumulation characteristics of different plants, 50 species (58 varieties) were grown in each of 6 large outdoor sand cultures supplied respectively with a trace (0.03 to 0.04 p. p. m.), 1, 5, 10, 15, and 25 p. p. m. of boron. The experiments were conducted at Riverside, Calif., during the period May 1930 to March 1934.

Approximately 25 percent of the plants made their greatest growth in the trace-boron culture, and the others responded to 1 p. p. m. or more of boron; the growth of a number of the species was increased by boron concentrations as high as 10 and 15 p. p. m.

Of the 58 varieties, 20 developed morphological symptoms of boron deficiency when grown in trace-boron, and the maturity of 4 varieties was markedly affected; 4 plants were more subject to mildew in trace-boron than in the higher concentrations.

The data provide a substantial basis for the conclusion that there is considerable overlapping between the injurious and the beneficial effects of boron within plants, inasmuch as mild to marked leaf injury was observed in 19 of the 72 plants (including repetitions) at or below the substrate concentrations that resulted in greatest growth.

The concentrations of boron in the leaves of plants (dry-weight basis) growing in 5-boron ranged from 58 to 1,804 p. p. m. and in 25-

boron from 209 to 3,875 p. p. m. The concentrations of boron in roots, stems, and fruit were generally much lower than those in the leaves; the concentrations of boron in entire plants tended to average about half of that in the leaves.

Numerical values for the tolerance of the plants to boron were derived by dividing the average of the dry weights in 5-, 10-, and 15-boron by the weight in trace- or 1-boron (whichever was higher) and multiplying this quotient by 100. These values ranged from below 10 for the highly sensitive plants to above 200 for one of the most tolerant plants.

Ratios of the concentration of boron in leaves (dry-weight basis) to boron in the trace-boron nutrient solution were usually between 400 and 1,200 and in 1-boron between 50 and 200. Lower ratios were found if the boron concentrations of the substrates were higher.

Little relation was found between boron tolerance and the boron-accumulation characteristics of different species.

Boron after entering the leaf tissues of most plants tends to remain there instead of being moved freely out, with sugars and other compounds, to growing tissues. The translocation of boron to the bark and wood and subsequently to the flesh of fruit takes place readily, however, in the stone fruits.

Comparisons between the boron concentrations in the sap expressed from frozen leaves and that estimated as possible in the sap on the basis of the moisture content and analyses of entire leaves indicated that all or nearly all of it was in solution in the leaves of 11 of the kinds tested and about half of it in 3 kinds. The accumulation of boron in leaves appears to be due to the formation of compounds with large or otherwise immobile molecules that are unable to diffuse through the plasma membranes.

A number of plantings grown during the winter months were repeated in summer. Higher concentrations of boron were found in winter-grown alfalfa and onions; but carrots, bluegrass, radishes, beets, and sweetclover accumulated more boron when grown in the summer.

Onions, radishes, and carrots accumulated several times as much boron in their roots, relative to the concentrations in the leaves, when grown in winter as when grown in summer. High light intensity and possibly the higher temperatures were seemingly unfavorable during the summer to the movement of boron from the leaves to other organs of these plants. The data suggest that boron after entering the mesophyll reacts with leaf-cell constituents, forming soluble but relatively immobile compounds. The extent to which boron is immobilized is evidently related to the intensity or to the average duration of light.

Boron deficiency of a number of the plants was most pronounced under the climatic conditions that restricted the movement of boron from the leaves to other tissues. The results indicate that factors affecting the movement and distribution of boron in the plant may be almost as important in determining boron requirements as the boron-supplying power of the substrate.

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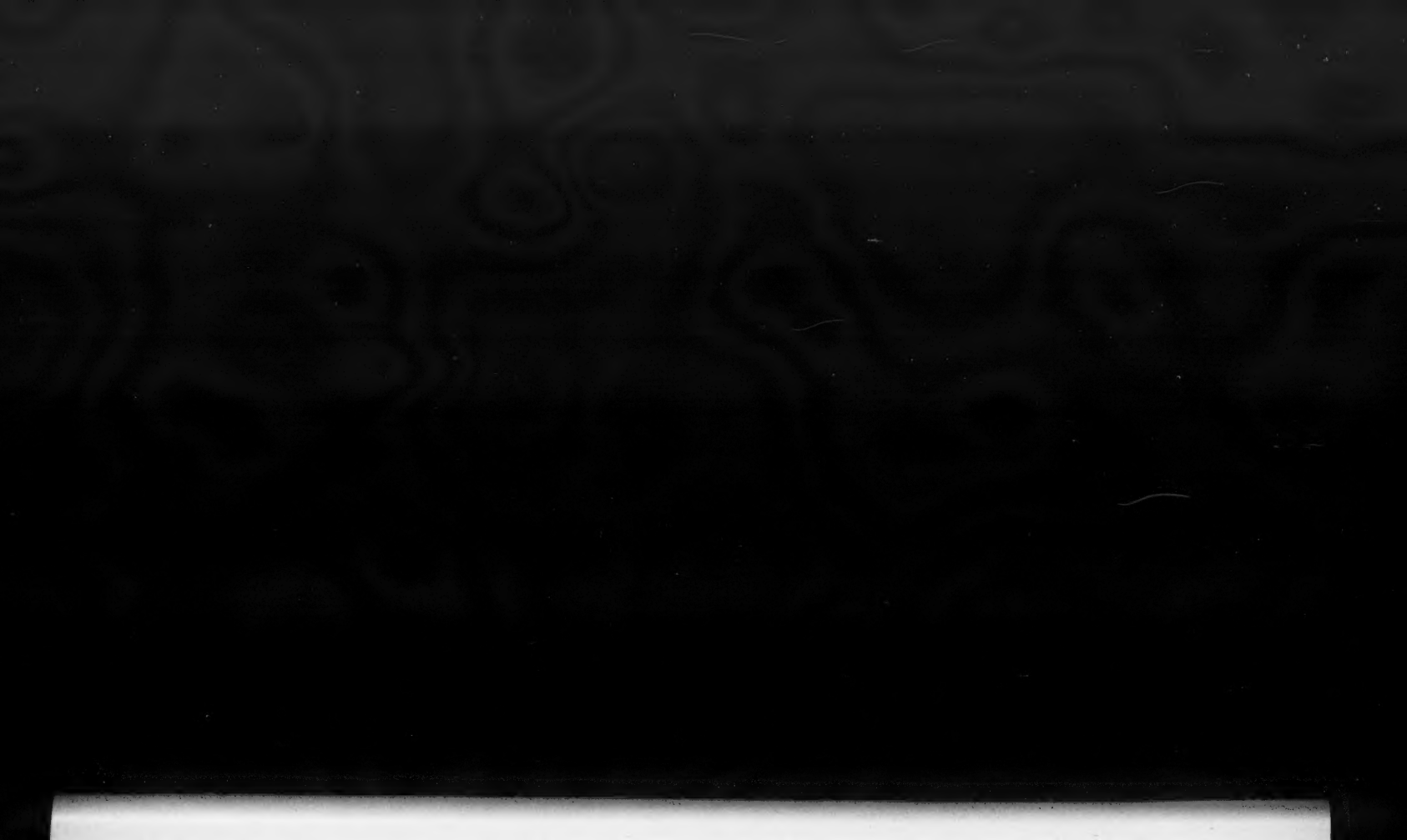
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